Climate Change and Forest Biodiversity in the Eastern United States: Insights from Inventory Data

by

Kai Zhu

Environment
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Alan E. Gelfand

Dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy in Environment
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ABSTRACT

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Abstract

Ecologists have long been interested in the relationships between climate change and forest biodiversity. For centuries, the scientific problems remain understanding the patterns of climate variation, forest geographic distribution, and demographic dynamics. Besides scientific merits, these questions will also help forest managers and policy makers to anticipate how forests respond to global change. This dissertation tackles these problems by using statistical modeling on climate and forest inventory data in the eastern United States.

In Chapter 1, we ask the question on the observed tree range distributions in response to contemporary climate change in the eastern United States. Tree species are expected to track warming climate by shifting their ranges to higher latitudes or elevations, but current evidence of latitudinal range shifts for suites of species is largely indirect. In response to global warming, offspring of trees are predicted to have ranges extend beyond adults at leading edges and the opposite relationship at trailing edges. Large-scale forest inventory data provides an opportunity to compare present latitudes of seedlings and adult trees at their range limits. Using the USDA Forest Service's Forest Inventory and Analysis data, we directly compared seedling and tree 5th and 95th percentile latitudes for 92 species in 30 longitudinal bands for 43,334 plots across the eastern United States. We further compared these latitudes with 20th century temperature and precipitation change and functional traits, including seed size and seed spread rate. Results suggest that 58.7% of the tree species examined show the pattern expected for a population undergoing range contraction, rather than expansion, at both northern and southern boundaries. Fewer species show a pattern consistent with a northward shift (20.7%) and fewer still with a southward shift (16.3%). Only 4.3% are consistent with expansion at both range limits. When compared with the 20th century climate changes that have occurred at the range boundaries

themselves, there is no consistent evidence that population spread is greatest in areas where climate has changed most; nor are patterns related to seed size or dispersal characteristics. The fact that the majority of seedling extreme latitudes are less than those for adult trees may emphasize the lack of evidence for climate-mediated migration, and should increase concerns for the risks posed by climate change.

In Chapter 2, we ask the question on tree abundance within geographic range responding to climate variation in the eastern United States. Tree species are predicted to track future climate by shifting their geographic distributions, but climate-mediated migrations are not apparent in a recent continental-scale analysis (Chapter 1). To better understand the mechanisms of a possible migration lag, we analyzed relative recruitment patterns by comparing juvenile and adult tree abundances in climate space. One would expect relative recruitment to be higher in cold and dry climates as a result of tree migration with juveniles located further poleward than adults. Alternatively, relative recruitment could be higher in warm and wet climates as a result of higher tree population turnover with increased temperature and precipitation. Using the USDA Forest Service's Forest Inventory and Analysis data at regional scales, we jointly modeled juvenile and adult abundance distributions for 65 tree species in climate space of the eastern United States. We directly compared the optimal climate conditions for juveniles and adults, identified the climates where each species has high relative recruitment, and synthesized relative recruitment patterns across species. Results suggest that for 77% and 83% of the tree species, juveniles have higher optimal temperature and optimal precipitation, respectively, than adults. Across species, the relative recruitment pattern is dominated by relatively more abundant juveniles than adults in warm and wet climates. These different abundance-climate responses through life history are consistent with faster population turnover and inconsistent with the geographic trend of large-

scale tree migration. Taken together, this juvenile-adult analysis suggests that tree species might respond to climate change by having faster turnover as dynamics accelerate with longer growing seasons and higher temperatures, before there is evidence of poleward migration at biogeographic scales.

In Chapter 3, we ask the question on the demographic dynamics of density dependence at the individual tree level in eastern US forests. Density dependence could maintain diversity in forests, but studies disagree on its importance. Part of the disagreement results from the fact that different studies evaluate different responses (per-seedling or per-adult survival or growth) of different stages (seeds, seedlings, or adults) to different inputs (density of seedlings, density or distance to adults). Most studies are conducted on a single site and thus are difficult to generalize. Using USDA Forest Service's Forest Inventory and Analysis data, we analyzed over a million seedling-to-sapling recruitment observations of 50 species for both per-tree (adult) and per-seedling recruitment rates, controlling for climate effects in eastern US forests. We focused on per-tree recruitment as it is most likely to promote diversity at the population level, and it is most likely to be identified in observational or experimental data. To understand the prevalence of density dependence, we quantified the proportion of species with significant positive or negative effects. To understand the strength of density dependence, we determined the magnitude of effects among conspecifics and heterospecifics, and how it changes with overall species abundance. We found that the majority of the 50 species have significant density dependence effects, mostly negative, on both per-tree and per-seedling recruitment. Per-tree recruitment is positively associated with conspecific seedlings, saplings, and heterospecific saplings, negatively associated with heterospecific seedlings, conspecific and heterospecific trees. Per-seedling recruitment is positively associated with conspecific and heterospecific saplings, but negatively

associated with conspecific and heterospecific seedlings and trees. Furthermore, for both per-tree and per-seedling recruitment, density dependence effects are stronger for conspecific than heterospecific neighbors. However, the strength of these effects does not vary with species abundance. We conclude that density dependence is pervasive, especially for per-tree recruitment, and its strength among conspecifics and heterospecifics is consistent with the predictions of the Janzen-Connell hypothesis.

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1 Failure to migrate: lack of tree range expansion in response to climate change

1.1 Introduction

Anticipating whether or not species range limits can track climate change is a goal of global change research (Clark *et al.*, 2001; Davis & Shaw, 2001; Jackson *et al.*, 2009; Loarie *et al.*, 2009; Dawson *et al.*, 2011). Across the globe, mounting evidence confirms widespread temperature increases, particularly at high northern latitudes (IPCC, 2007). In the eastern United States, mean annual temperatures increased during the 20th century in the Midwest and Northeast, but not in the Southeast, where warming summers were balanced by cooling winters (Figure 1.1a). When viewed in terms of a velocity, as has been advocated recently (Loarie *et al.*, 2009), regions in the Northeast and Upper Midwest have seen climate shifts of more than 100 km during the 20th century (Figure 1.1b). As the climate warms, new regions that become available for occupation may be colonized as those no longer suitable are abandoned. Inevitable time lags involved in plant dispersal, colonization, establishment, and maturation threaten not only rare species, but also many that are abundant and provide vital ecosystem functions and services. Numerous data sets and models suggest a variety of species' responses to changing climate, but robust empirical evaluation remains challenging.

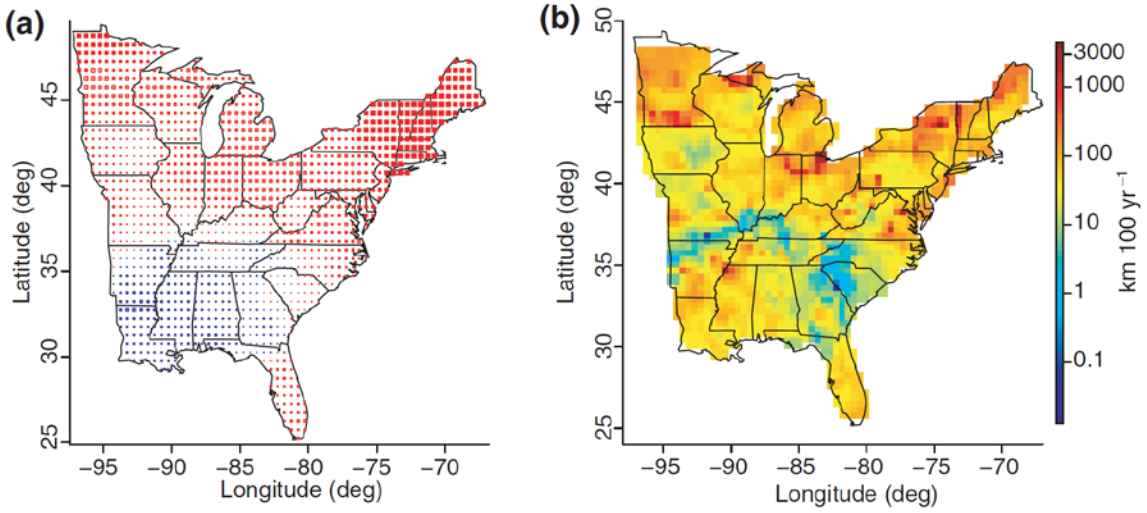

Figure 1.1: Temperature change in time and space during the 20th century in the eastern United States. Data are extracted from 10 decadal mean annual temperatures from the Climate Research Unit (CRU) data set (Mitchell & Jones, 2005). (a) is the temporal trend during 1901 – 2000, with squares denoting the slope of the linear regression of decadal data: red – increasing trend, blue – decreasing trend; solid – significant slope with $p < 0.05$, open – insignificant slope with $p > 0.05$; and square size being proportional to the absolute value of the slope. (b) is the spatial velocity of temperature change, defined as the quotient of the temporal gradient (a) and the north-south directional spatial gradient in 1991 – 2000 of temperature distribution (Loarie *et al.*, 2009).

Previous studies generally agree that plants will respond to climate warming by shifting their ranges to higher elevations and latitudes (Hughes, 2000; McCarty, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Parmesan, 2006; Chen *et al.*, 2011), but only elevation responses are thus far readily apparent in data (Beckage *et al.*, 2008; Holzinger *et al.*, 2008; Kelly & Goulden, 2008; le Roux & McGeoch, 2008; Lenoir *et al.*, 2008; Bergamini *et al.*, 2009; Crimmins *et al.*, 2011; Van Bogaert *et al.*, 2011). The most recent comprehensive meta-analysis by Chen *et al.* (2011) does not include latitudinal range shifts of plants. In fact, studies of plant latitudinal range boundaries rely heavily on models at global (Thomas *et al.*, 2004), continental (Bakkenes *et al.*, 2002; Thuiller *et al.*, 2005; Meier *et al.*, 2011), and regional scales (Midgley *et al.*, 2002; Broennimann *et al.*, 2006). Species distribution models in general (Guisan & Thuiller,

2005; Elith & Leathwick, 2009), and bioclimatic envelope models in particular (Pearson & Dawson, 2003; Heikkinen *et al.*, 2006) provide valuable perspectives on potential effects of climate change (Botkin *et al.*, 2007; McMahon *et al.*, 2011). However, there is little empirical evidence to support the model predictions that populations are shifting to higher latitudes.

The Forest Inventory and Analysis (FIA) program of the USDA Forest Service provides an extensive tree inventory for examining tree species range distribution and migration from millions of observations across the country. FIA conducts the only systematic sampling of all forest tree species at a continental scale. Although this database has been extensively used in tree range projection models (Iverson *et al.*, 2004; Iverson *et al.*, 2008), it has been used to evaluate potential range shifts only in highly indirect ways. Using FIA data, Murphy *et al.* (2010) found that 60% of 102 eastern US tree species have peak abundances of fitted distributions in the northern portion of their ranges. They suggested that this pattern could reflect range contraction in the south and limited expansion in the north. If ranges are more strongly limited by climate at high rather than low latitudinal limits (Dobzhansky, 1950; MacArthur, 1972; Brown *et al.*, 1996), then the opposite pattern could be expected, with strong advance in the north and limited response in the south, depending on the effects of competition with invaders advancing from the south. In addition to analyzing abundance, Woodall *et al.* (2009) compared the mean latitude of seedling and tree occurrence using FIA data throughout the eastern United States and found that northern species tend to show a shift northward, while southern species do not. They recognized that these conclusions could be affected by their specific choice of study species (Woodall *et al.*, 2010) and their use of mean latitude, which reflects central tendency rather than range limits. Combining FIA, climate, geographic data, and several emission scenarios, Iverson *et al.* (2008) predicted that the center of suitable habitats for 134 eastern US tree species would move up to 800 km

northeast. For five of the common species they analyzed, Iverson *et al.* (2004) predicted that migration in the next century will extend no more than 20 km beyond their current northern range. Taken together, these different approaches suggest that trees might be responding to climate change with latitudinal range shifts, but the evidence is indirect and not in clear agreement. The influence of global climate change on range boundaries could benefit from development of new techniques to exploit the FIA evidence at range boundaries across large spatial scales.

In this study, we develop a novel technique for examining the latitudinal difference between offspring and adults of trees at both northern and southern range limits across the eastern United States, and we evaluate the number of species showing evidence for range expansion or contraction. We then compare these patterns with changes in 20th century temperature and precipitation, as well as functional traits expected to influence migration potential, specifically, seed size and dispersal properties. We test the widely held hypothesis that trees could track climate change by migration, showing differences between offspring and adult range limits (Neubert & Caswell, 2000; Lewis *et al.*, 2006), with the largest differences between offspring and adult extent being in areas where climate change has been most pronounced. There has been substantial effort in recent years to determine whether small-seeded species have greater migration potential than large-seeded species (reviewed by Angert *et al.*, 2011). Four mutually exclusive and all-inclusive hypotheses are summarized by a four-quadrant diagram of range shifts at northern and southern frontiers (Figure 1.2):

1. Overall range expansion: if a species is expanding at northern and southern frontiers, then offspring will have greater latitudinal extent than adults at both range limits (I in

Figure 1.2), as would occur if the environment is changing in ways that benefit the species in both areas.

2. Northward range shift: if a species is expanding at northern frontiers and retreating from southern frontiers, then offspring will extend north of adults at the northern range limit, and adults will extend south of offspring at the southern range limit (II in Figure 1.2). This is the expected response to climate warming.
3. Overall range contraction: if a species is contracting from northern and southern frontiers, then offspring will have less latitudinal extent than adults at both range limits (III in Figure 1.2), as would occur if the environment is changing in ways that harm the species or benefit its competitors in both areas.
4. Southward range shift: if a species is retreating from northern frontiers and expanding at southern frontiers, then adults will extend north of offspring at the northern range limit, and offspring will extend south of adults at the southern range limit (IV in Figure 1.2).

We further evaluate the hypotheses that species with greater dispersal ability might spread more rapidly under climate change (Clark *et al.*, 2001; Angert *et al.*, 2011; Nathan *et al.*, 2011), and small-seeded species might show greater northward (II) or southward (IV) range shifts than large-seeded species (near the origin in Figure 1.2).

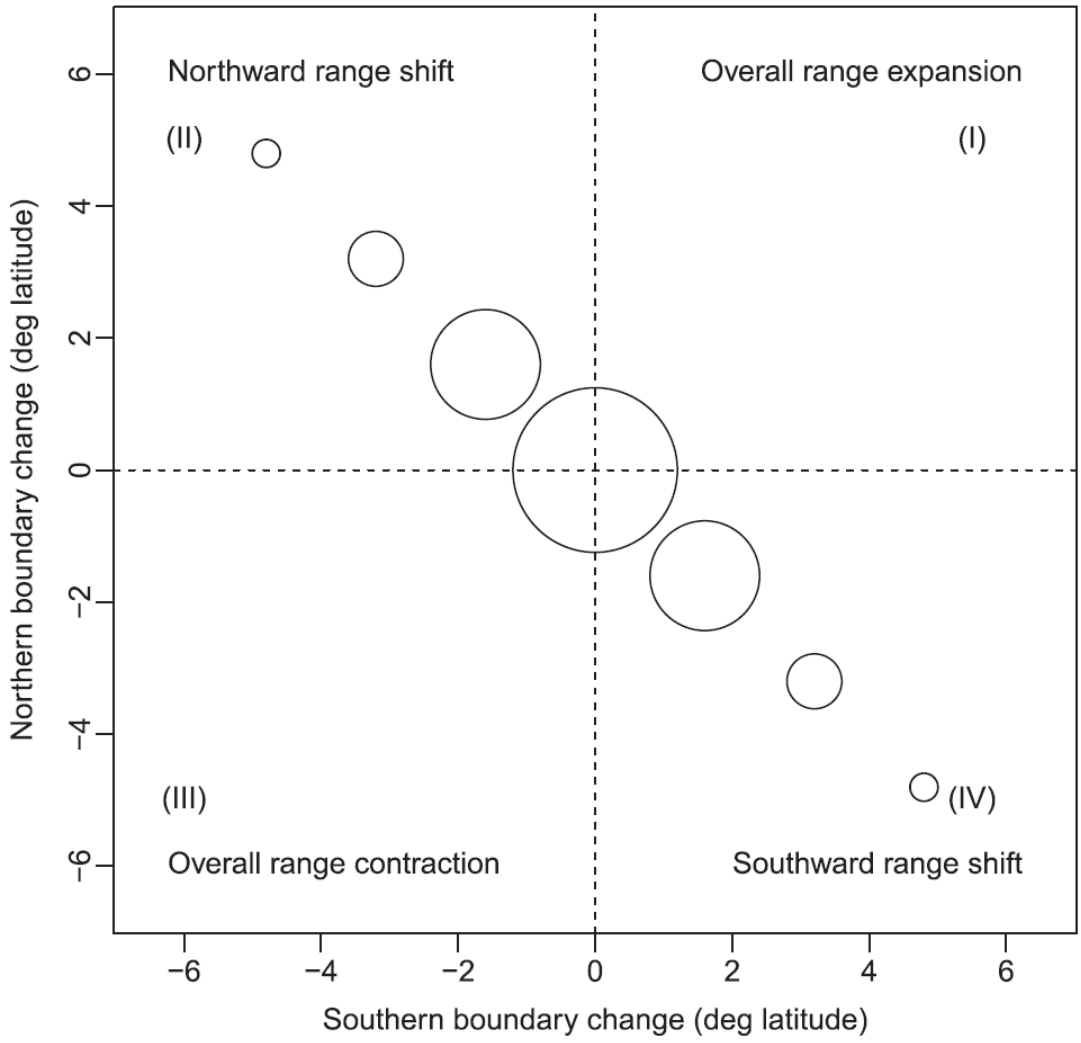

Figure 1.2: Four-quadrant schematic diagram of species having greater latitudinal extent for offspring than adults (I) both at northern and southern range limits, suggesting overall range expansion; (II) at northern but not southern range limits, suggesting northward range shift; (III) at neither northern nor southern range limits, suggesting overall range contraction; (IV) at southern but not northern range limits, suggesting southward range shift. In both horizontal and vertical axes, positive value means the tendency of range expansion, while negative value means the tendency of range contraction. Each circle is a species drawn with an arbitrary center, and the diameter is proportional to the seed size, as we expect small-seeded species tend to track climate change, showing northward (II) or southward (IV) range shift, while large-seeded species tend to have no change in range limits (near the origin).

While providing perhaps the most direct evidence for subcontinental scale range shifts for a large number of species, it is important to recognize limitations of FIA data, and the fact that no analysis can definitively determine migration patterns. We compare results of our analysis with other empirical and modeling studies, recognizing how sampling designs, successional trends, and source-sink dynamics can influence study of adult and offspring distributions.

1.2 Materials and methods

Our analysis concerns the latitudinal extent of offspring and adults from FIA data distributed longitudinally across the eastern United States, combined with 20th century temperature and precipitation change, as well as seed size and dispersal properties. A population that is migrating north in response to warming is expected to have offspring extending to higher latitudes than adults in regions that have warmed over the last century, but not in regions where climate has remained essentially constant. This is the signature of an expanding population front, as predicted by all models of migration (Okubo, 1980; Neubert & Caswell, 2000; Clark *et al.*, 2001; Lewis *et al.*, 2006). Likewise, a population retreating from a warming southern boundary is expected to have adults south of the southern extent of new recruitment by offspring. This is the basic assumption behind recent analyses of Woodall *et al.* (2009), but analyzed in our study at the range boundaries themselves. Lenoir *et al.* (2009) used this assumption when comparing seedling and adult distributions to detect altitudinal range shifts. In the following sections we summarize our methods, including the FIA sampling design, the longitudinal band analysis (LBA) to detect range shifts, and comparisons of range shifts, climate change, and functional traits.

1.2.1 Forest inventory data

The FIA program is the primary source for information on the extent, condition, status, and trends of forest resources in the United States (Smith *et al.*, 2009). FIA applies a nationally consistent sampling protocol covering all ownerships across the United States, resulting in national sample intensity of one plot per 2,428 ha (Bechtold & Patterson, 2005) within forest lands (i.e., homogenous forest cover classes to reduce estimate uncertainty). Sample intensities vary somewhat by state; however, because the inventory is systematic, varying sample intensities do not bias assessment of tree species locations (McRoberts *et al.*, 2005). Forested land is defined to be greater than 0.4 ha in area and 36.6 m in width, with at least 10% tree cover. FIA inventory plots in forested conditions consist of four 7.2 m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Bechtold & Patterson, 2005). All trees (standing live and dead) with a diameter at breast height (DBH) of at least 12.7 cm, are inventoried on forested subplots. Within each subplot, a 2.07 m radius microplot offset 3.66 m from subplot center is established where only live trees with a DBH between 2.5 and 12.7 cm are inventoried. Within each microplot, all live tree seedlings are tallied according to species. Conifer seedlings must be at least 15.2 cm in height with a root collar diameter less than 2.5 cm. Hardwood seedlings must be at least 30.5 cm in height with a root collar diameter less than 2.5 cm. Inherent in any large-scale forest inventory, there is measurement error associated with tree species identification. The FIA program has a quality assessment and quality control program associated with the national inventory that monitors measurement error and continuously seeks to reduce said errors (Pollard *et al.*, 2006; USDA Forest Service, 2011). Nationally, FIA field crews have attained at least 95% repeatability of tree species identification with nearly 9% of all inventory plot measurements remeasured for this repeatability assessment (*ca.* 2010).

In this analysis, FIA data were extracted from annual inventories (1999 to 2008) in 31 eastern states for a total of 43,334 inventory plots from FIADB version 4.0 on March 16, 2010 (available online http://fia.fs.fed.us/; Figure 1.3). Because we focus on range limits, we used Little's digitized geographic range maps (USGS, 1999) to restrict analysis to the 92 species having their entire geographic range within the eastern United States (Table A1 includes the complete species list). To compare species in different life stages (offspring vs. adult), we followed the FIA definition, dividing the data into two types of subgroups: (i) seedling (DBH < 2.5 cm) vs. tree (DBH ≥ 2.5 cm), and (ii) sapling (2.5 cm ≤ DBH < 12.7 cm) vs. large tree (DBH ≥ 12.7 cm). In other words, we conducted two offspring vs. adult comparisons: seedling vs. tree, and sapling vs. large tree.

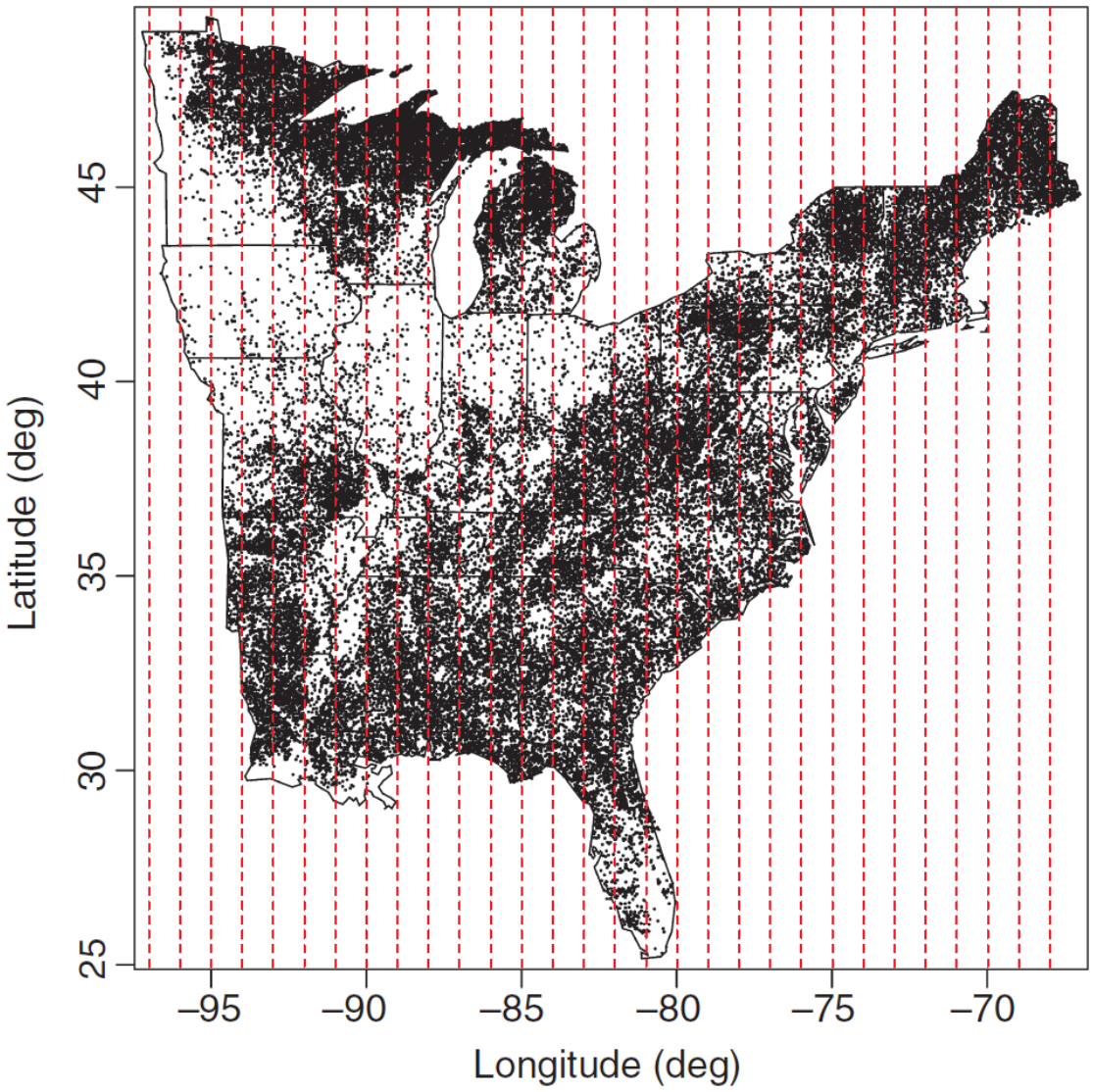

Figure 1.3: Approximate Forest Inventory and Analysis (FIA) plot locations (black points) and one degree longitudinal study bands (red dashed lines) in the eastern United States.

1.2.2 Longitudinal band analysis

We developed a longitudinal band analysis (LBA) for comparing occurrences of offspring vs. adults across the full northern and southern frontiers for each species. To allow for variation in migration response along range limits, we stratified the 43,334 FIA plots into

longitudinal bands 1° wide, from 98° W to 68° W spanning the geographic extent of the eastern United States (Figure 1.3). For each longitudinal band, we determined the 5th and 95th percentiles of latitudinal occurrence for all species for each of the life stages (seedling vs. tree, and sapling vs. large tree). In other words, 5% of the occurrences are at lower latitudes than the 5th percentile and at higher latitudes than the 95th percentile. The distributions of these percentiles across longitudinal bands were compared between stages to evaluate the assumption that offspring distributions extend to higher or lower latitudes than adults. We calculated the difference for longitudinal pairs of offspring and adults, yielding latitudinal difference distributions (LDD) at northern and southern boundaries for each species. For the x^{th} latitudinal percentile,

$$\mathrm{LDD}_{j,x} = q_{j,x}^{(\mathrm{offspring})} - q_{j,x}^{(\mathrm{adult})} \qquad 1$$

where $q_{j,x}$ is the latitude corresponding to percentile x in longitudinal band j. At a northern frontier, positive $\mathrm{LDD}_{j,x}$ is consistent with northern expansion, because it implies that offspring extend further north than adults. At a southern frontier, positive $\mathrm{LDD}_{j,x}$ is consistent with northward retreat (southern contraction). The mean of LDD at a range boundary (north or south) summarizes the mean latitudinal difference between small and large size classes. For each species, we summarized two mean LDD values, one at northern and one at southern frontiers.

With this explanation of the LBA method, underlying motivation is straightforward. Our analysis of offspring and adult latitudinal extents is fundamentally an examination of distributional extremes. The extreme value of a distribution has no statistical confidence assigned to it, because it is observed once. Likewise, a comparison of locations for the extreme offspring latitude with the extreme adult latitude has no statistical uncertainty associated with it. However, by comparing these extreme events from a number of longitudinal bands (i.e., the LDDs of

Equation 1) we introduce replication and the potential to evaluate the relationship between offspring and adults along their range margins across areas that have experienced different degrees of 20th century warming (Figure 1.1). It further introduces the potential for modeling, as LDDs may depend on the degree of climate change or other variables associated with each band (next section). To evaluate sensitivity to a specific percentile, we repeated the analysis not only for the 5th and 95th percentiles of latitudes, but also for north and south extremes (the 0th and 100th percentiles), and the 10th and 90th percentiles. The sensitivity to discretizing longitude was assessed by repeating the analysis at 0.5°, 1°, and 2° wide longitudinal bands.

1.2.3 Climate change and functional trait data

To determine if the tendency to expand or contract is related to the degree of climate change in a region, we compared the mean of LDD with 20th century climate change from the Climate Research Unit (CRU) high resolution climate data, version 2.1 (Mitchell & Jones, 2005). Based on more than seven sources of meteorological station records, the CRU data is gridded with a spatial resolution of 0.5° × 0.5°, and temporal resolution of 10 decades (1900 to 2000). Analysis was completed for the two most commonly used climate variables, mean annual temperature and mean annual precipitation. We first calculated 20th century linear trends (slopes) for temperature and precipitation change for each longitudinal band location $q_{j,x}$ in Equation 1. For each species, we determined the correlation between LDD and trends in temperature or precipitation,

$$\begin{aligned} \rho_T &= \mathrm{cor}\left(\mathrm{LDD}_{j,x}, \Delta T\left(q_{j,x}\right)\right) \\ \rho_P &= \mathrm{cor}\left(\mathrm{LDD}_{j,x}, \Delta P\left(q_{j,x}\right)\right) \end{aligned} \qquad 2$$

where ΔT is temperature change and ΔP is precipitation change for offspring locations ($q_{j,x}$). At the northern frontier, positive ρ_T (ρ_P) is evidence that range expansion occurs where temperature (precipitation) increase has been greatest. At the southern frontier, positive ρ_T (ρ_P) is evidence that range contraction occurs where temperature (precipitation) increase has been greatest. We used correlation for these comparisons, because there was no evidence of nonlinearity.

The correlations between climate change and spread can be made more transparent by placing them on the same dimensions, translating climate change over time to climate velocity (Loarie *et al.*, 2009). Over much of the eastern US canopy forests date from the early 20th century. Seedlings in our data sets established approximately a century later. The velocity of climate change with latitude y is obtained from rate of change and the climate gradient (Figure 1.1b),

$$\frac{dy}{dt} = \frac{dT}{dt} \Big/ \frac{dT}{dy} \qquad 3$$

We compared the mean LDD value for each species with the velocity of climate change at its range limit.

To determine whether or not dispersal characteristics can explain the tendency to expand or contract, as being hypothesized in recent studies (Angert *et al.*, 2011; Nathan *et al.*, 2011), we compared mean LDD from the LBA method with plant functional trait data from the USDA Natural Resources Conservation Service's PLANTS database (USDA NRCS, 2010). We compared range expansion or contraction potential with two functional traits: (i) seed size, which is the reciprocal of seed per pound in an average seed lot; and (ii) seed spread rate, which is an ordinal variable (slow, moderate, or rapid) intended to describe the capability to spread compared with other species with the same growth habit (USDA NRCS, 2010).

All analyses were performed in R version 2.12.1 (R Development Core Team, 2010).

1.3 Results

Use of LBA to identify relationships consistent with range shifts is illustrated by example species, followed by summaries for the entire data set. LDDs from the seedling vs. tree comparison (Equation 1) show contrasting patterns for two species at northern range limits (Figure 1.4): expansion for *Ilex opaca* (American holly) and contraction for *Diospyros virginiana* (common persimmon). For *Ilex opaca*, seedlings (red) occur well north of the range for trees (blue; Figure 1.4a and b). If the northern extent of seedlings represents a sink population, then seeds are dispersed to and germinate at these latitudes, but do not survive to adulthood. This would occur, for example, if temperatures were too low to support populations of the species (e.g., bird-dispersed seeds germinate but do not survive). An alternative explanation is that the range is expanding. It is unlikely that seedlings could long survive winter temperatures too low to support adult trees. Note that this is not one of the horticultural species of *Ilex* typically sold in nurseries. It is thus possible that *Ilex opaca* has expanded its range to take advantage of warming climate in the upper Midwest (Figure 1.1a).

A contrasting pattern was found for *Diospyros virginiana* (Figure 1.4c and d). Seedlings (red) do not extend as far north as trees (blue), as would be expected for a range contraction. This pattern is apparent across the full northern frontier, from Missouri to Delaware. Current information does not identify whether lack of *Diospyros* seedlings at the northern frontier results from recent climate change, land use change, or other factors. These direct comparisons were extended to all the study's 92 species.

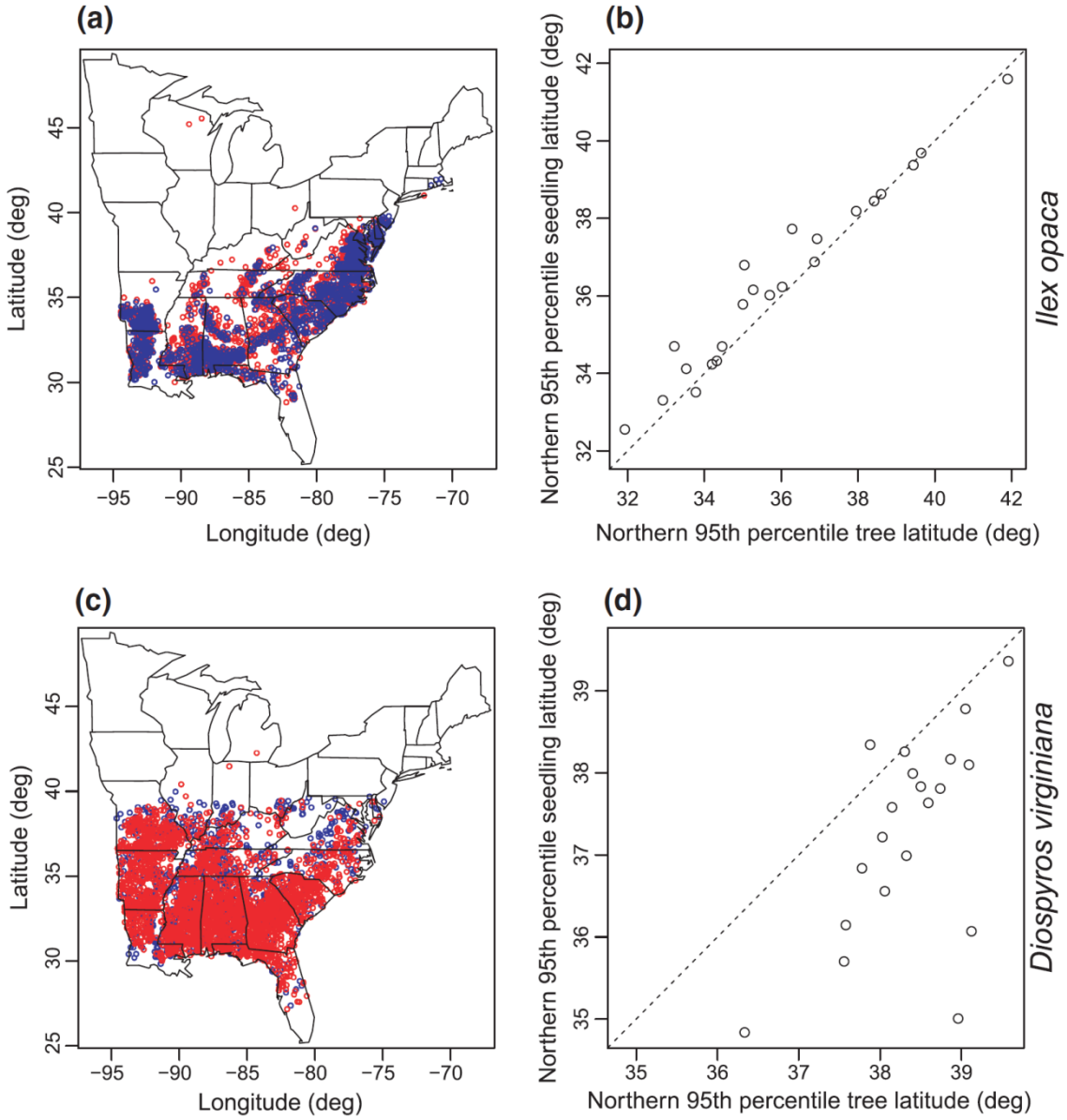

Figure 1.4: Seedling and tree range difference at the northern range limit of two example species, *Ilex opaca* (a, b) and *Diospyros virginiana* (c, d). (a) and (c) show all plot locations of seedlings (red) and trees (blue). (b) and (d) show the differences between seedling and tree 95th percentile latitudes in each longitudinal band. Points above the 1:1 line in *Ilex opaca* (b) indicate longitudinal bands where seedlings are located further north than trees, as would be expected if there is expansion at the northern range limit. Points below the 1:1 line in *Diospyros virginiana* (d) indicate longitudinal bands where trees occur further north than seedlings, as would be expected if there is contraction at the northern

range limit. For clarity in the figure, seedlings (red) are overlaid with trees (blue) in *Ilex opaca* (a), while trees (blue) are overlaid with seedlings (red) in *Diospyros virginiana* (c).

Across all species, patterns consistent with range contraction at both northern and southern boundaries predominate. This pattern is especially pronounced for the seedling vs. tree comparison, but it is also evident for the sapling vs. large tree comparison. The quadrant diagram (Figure 1.5) shows species having greater latitudinal extent for seedlings than trees at both northern and southern range limits (I), at northern but not southern range limits (II), at neither northern nor southern range limits (III), or at southern but not northern range limits (IV). The largest proportion of species has lower seedling latitudinal extent than trees at northern boundaries, and higher latitudinal extent than trees at southern boundaries—in other words, contraction at both boundaries. In the seedling vs. tree comparison, 54 out of 92 species (58.7%) show this pattern consistent with range contraction (III in Figure 1.5). In the sapling vs. large tree comparison, 60 out of 92 (65.2%) species show this pattern (Figure A1).

The other three cases contain fewer species (Figure 1.5). In the seedling vs. tree comparison, 19 out of 92 species (20.7%) are consistent with range expansion in the north and contraction in the south (II in Figure 1.5), while 15 out of 92 species (16.3%) are consistent with range expansion in the south and contraction in the north (IV in Figure 1.5). In other words, slightly more species are consistent with a northward range shift (II in Figure 1.2) than with a southward range shift (IV in Figure 1.2). In the sapling vs. large tree comparison, 12 out of 92 species (13%) show the pattern consistent with northward range shift, and 16 out of 92 species (17.4%) show the pattern consistent with southward range shift (Figure A1).

Evidence consistent with expansion at both northern and southern limits is least well represented. Only four out of 92 species (4.3%) have lower 5th and higher 95th percentiles for

seedlings than for trees (I in Figure 1.5). The same percentage (4.3%), albeit a different set of four species, was obtained for comparisons of saplings vs. large trees (Figure A1).

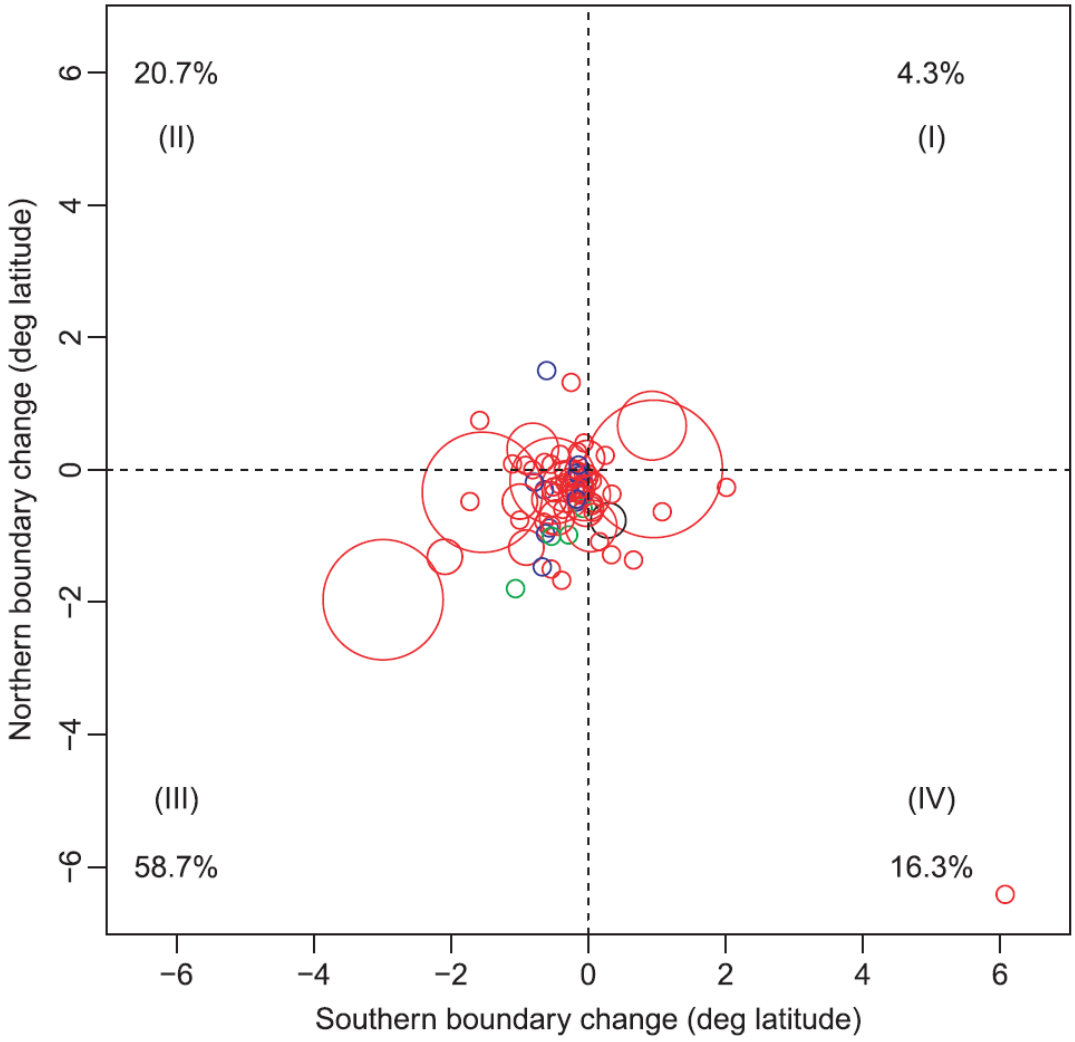

Figure 1.5: Latitudinal range change at southern (5th percentile) and northern (95th percentile) boundaries from the seedling vs. tree comparison. Four quadrats bear the same meaning as Figure 1.2. Each circle is a species, scaled to its seed size, with the color of seed spread rate (red, slow; blue, moderate; green, rapid; black, no data) from PLANTS database (USDA NRCS, 2010). Percentages in the four quadrats summarize the proportion of species falling into the corresponding cases. Detailed latitudinal differences for all species are shown in Table A1.

In sum, our results suggest a pattern consistent with the following ranking in terms of number of species: overall range contraction > northward or southward range shift > overall range expansion. For species having comparisons consistent with range contraction, the magnitude of the latitudinal shift is greater for the seedling vs. tree than for the sapling vs. large tree comparisons. This result is robust, being consistent across 0.5°, 1°, and 2° longitudinal bandwidths and for percentiles 0^{th} and 100^{th} (maximum and minimum), 5^{th} and 95^{th}, and 10^{th} and 90^{th}. Across all 92 species the average range contraction was 0.37° (42 km) at northern boundary, and 0.26° (29 km) at southern boundary for the seedling vs. tree comparison.

The relationship between LDD and 20^{th} century climate trends (Equation 2) shows a similar pattern for both offspring vs. adult comparisons. For the seedling vs. tree comparison, 62.2% of species have positive ρ_T at northern limits, implying that ranges expanded most where temperature increase was greatest, and 44.4% have positive ρ_T at southern limits, implying that ranges contracted most where temperature increase was greatest. For the sapling vs. large tree comparison, these percentages are 61.1% and 44.4%, respectively (Table A2). There was no relationship between expansion patterns and precipitation change.

Contrary to the common assumption that migration potential is determined by seed characteristics, the LBA shows no relationship between range expansion or contraction and functional traits (i.e., seed size and seed spread rate). Most species classified as large seeded and slow spread potential fall in the category of overall reduction in range size (circle sizes and colors in III of Figure 1.5). Small seeded species occur in all four categories, including overall range expansion or contraction and northward or southward range shift.

1.4 Discussion

Despite caveats that must apply to any analysis of forest plot data, evidence for climate-driven migration is essentially absent in this large analysis that considers distributions of offspring and adults across geographic gradients in climate change. Patterns are more consistent with range contraction of eastern US tree species than with northward migration. The results based on the direct comparisons of seedlings and trees at range limits do not inspire confidence that tree populations are tracking contemporary climate change. If the seedling class integrates up to a decade or more of climate history (seedling banks range up to several decades in age), and trees integrate up to a century, then northward migration in response to warming would result in seedlings displaced to the north of mature individuals of the same species. The greater the warming, the greater the expected displacement. Likewise, retreat from southern boundaries is expected where warming has reduced the competitive advantage previously enjoyed in a cooler climate. This assumption is the basis for a large number of analyses of climate and migration (Okubo, 1980; Neubert & Caswell, 2000; Clark *et al.*, 2001; Lewis *et al.*, 2006), but massive inventories of both seedlings and adults have not been analyzed in this way. The majority of species in our analysis shows a pattern consistent with range contraction at both northern and southern range limits. Some species are consistent with the expected but much debated poleward range shift (Parmesan & Yohe, 2003; Chen *et al.*, 2011). Range expansion at both northern and southern frontiers is observed for the smallest proportion of species among the four possible cases (Figure 1.5). Due to FIA's sampling intensity, this study provides perhaps the most robust assessment of tree migration potential. Moreover, failure to find evidence that seedlings extend as far north as adults and absence of a relationship to local climate changes suggests cause for

concern, given the temperature trends already underway during the 20th century (Figure 1.1). Before discussing implications we consider some of the important caveats of an analysis like this.

1.4.1 Sources of uncertainty, limitations, and caveats

The factors that could influence patterns we quantified here include (i) sampling effects and data limitations, (ii) successional changes, and (iii) sink populations beyond the range where the population is viable. The caveats that follow could apply to any of the many recent studies reporting evidence of range shifts, but are rarely considered.

Due to the inherent limits of FIA data (Woodall *et al.*, 2009), the comparison of the presence/absence data could be biased if there is a higher probability of finding offspring than adults or vice versa. Our analysis that includes not only seedlings and trees, but also saplings and large trees (see 1.2.1), reduces this risk—our results are similar for both comparisons. We further relied on the fact that the sample size is massive. A range of different stand ages will contribute variation to patterns we analyze, but not necessarily overwhelm them. The large sample sizes for both seedlings and trees can help to overcome bias toward particular life stages. However, the fact that sample sizes are substantial does not insure that plot design can be ignored. The 54 m^2 seedling sample area is still much smaller than the 673 m^2 tree plot (Bechtold & Patterson, 2005), but seedlings can occur at much higher densities.

It is important to consider whether or not there are non-climatic obstacles to migration. Species faced with physiographic barriers to migration (e.g., close to coastlines, parent material heterogeneity, and mountains) should be interpreted carefully, because they may be more limited by geography than climate (Bakkenes *et al.*, 2002; Clark *et al.*, 2011b). Species with range limits close to boundaries of the sample region may bias results. Our analysis includes few northern species, because they may extend their ranges into Canada. Careful attention to caveats yields

conclusions robust to the widths of longitudinal bands (0.5°, 1°, or 2°), or the latitudinal percentiles (0^{th} and 100^{th}, 5^{th} and 95^{th}, or 10^{th} and 90^{th}).

The possibility that successional change and sink populations could be mistaken for range expansion has to be considered as an alternative explanation. Seedlings can expand in areas where trees are rare or absent as successional species reinvade or recruitment declines with stand development. Successional changes could affect our results in at least two ways. Light demanding species can be common in forest overstories where recruitment of the same species in shaded understories is rare. Alternatively, early successional stands could support recruitment of light-demanding species at sites where few individuals have reached the adult stage. In both cases, a biased representation of particular stand ages could affect results in ways that are difficult to anticipate. There is also potential for interactions. Presence of seedlings following recovery from disturbance would be especially confusing if there were a strong correlation between recent disturbance and climate change. Although there is substantial heterogeneity in land use across the eastern United States, much of the entire region is dominated by 20^{th} century afforestation. We expect that land cover has contributed to patterns we report, but we are unaware of systematic geographic trends could explain our results. We examined LDD by shade-tolerance classes and did not find a tendency for shade tolerant species to be expanding more than shade intolerant species.

Heterogeneous habitats may create sink populations for seedlings, outside the range of adult trees being supported by continual seed inputs (Pulliam, 1988). While possible in principle, the bulk of seed for most species falls close to adults and long-distance dispersed seed faces competition from copious seed produced by local plants. Moreover, seedlings may be more sensitive to climate variation than adults (Grubb, 1977; Harper, 1977). Thus, although we cannot

ignore the possibility of sink populations, we assume that such effects would not dominate the broad geographic patterns we report. If there are sink populations, our method would mistake them for range expansion. In other words, sink populations could not be an explanation for failure to find the range shifts predicted by climate change.

1.4.2 Comparison with other FIA studies

By directly analyzing tree and seedling distributions at range boundaries, our analysis of latitudinal extent addresses limitations of previous studies. Previous analyses using FIA data suggest that both seedlings and trees have higher abundance in the northern latitudes than the southern latitudes within their geographic ranges, which could be interpreted as a signature of northward tree migration (Woodall *et al.*, 2009; Murphy *et al.*, 2010), but could also represent responses to a whole range of variables. Abundance and occupancy patterns (Murphy *et al.*, 2006; Murphy *et al.*, 2010) might not provide evidence of range shifts, because geographic range is defined by boundaries, not abundance or occupancy within boundaries (Cox & Moore, 2010, pp. 204, 38-40). Despite different approaches and assumptions, Murphy *et al.* (2010) suggested that the most common response could be range contraction in the south and limited expansion in the north, leading to a possible overall range size reduction.

Woodall *et al.*'s (2009) comparison of mean latitudes for seedlings and trees could likewise miss dynamics at population frontiers. Range shifts in response to climate change are expected to occur at the leading (northern) or the trailing (southern) edges, with the changes in mean latitude being sensitive to other factors. Woodall *et al.* (2009) also examined maximum and minimum latitudes. Still, Woodall *et al.*'s (2009) results are consistent with range contraction in this analysis. At the southern range limits of northern species, 12 out of 15 species show greater

minimum latitude for seedlings. At the northern range limits of southern species, 10 out of 15 species show greater maximum latitude for trees (table 2 in Woodall *et al.*, 2009). Many of the 40 species they studied have ranges that are not contained within the eastern United States (especially for northern species), so dynamics at northern range limits are unknown (Woodall *et al.*, 2010). To minimize these effects on the analysis we included all species having entire ranges within the study area (see 1.2.1).

Climate change has already been large (Figure 1.1)—we do not have to wait decades to evaluate whether or not climate change is affecting migration. Our finding that the majority of species may experience range contraction at both northern and southern limits does not square with the expectation that species will migrate rapidly north in response to climate change. Many models predict rapid tree migration (Clark, 1998; McKenney *et al.*, 2007), but some do not (Clark *et al.*, 2001; Clark *et al.*, 2003; Nathan *et al.*, 2011). Iverson *et al.*'s (2008) habitat distribution model predicts that 61 to 68 of 134 species will increase at least 10%, and 50 to 58 species will lose at least 10% of their area-weighted importance value. Some of these predictions are consistent with our comparisons of offspring and adults (e.g., *Acer nigrum* and *Juglans cinerea*). On the other hand, Iverson *et al.* (2004) predicted that migration potential at northern range limit for *Diospyros virginiana*, *Liquidambar styraciflua*, *Oxydendrum arboreum*, *Pinus taeda*, and *Quercus falcata* would be limited to within 20 km of the area currently occupied. Our analysis of these species all show contraction at northern limits, in general agreement with Iverson *et al.*'s (2004) expectation that migration potential is limited.

1.4.3 Relationship with climate change and functional traits

The fact that most species appear to be contracting at both northern and southern range limits is not consistent with the expectation that temperature change during the 20th century

should allow for rapid spread (Figure 1.6). At the northern frontier, in particular, calculations using climate observations suggest that species may need to migrate hundreds of km northward to track warming temperatures in the eastern United States (Figure 1.1b). However, making the reasonable assumption that the LDD observed in this study represents dynamics on a 100 yr scale, our results suggest that most species have not tracked 20th century temperature change (below the 1:1 line in Figure 1.6).

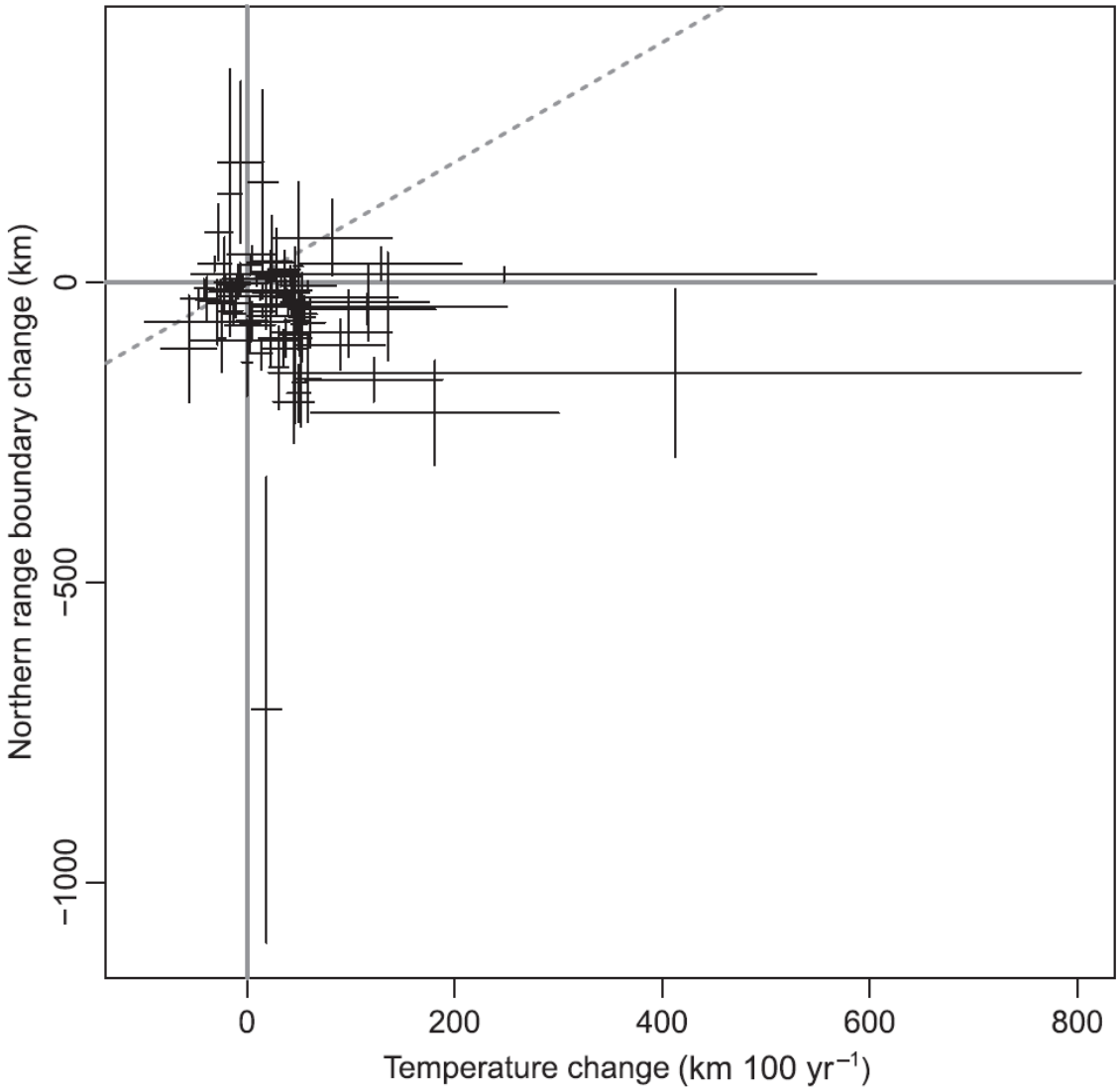

Figure 1.6: Temperature change during the 20th century (calculated as Figure 1.1b) in comparison with latitudinal difference between seedlings and trees at northern range boundary (calculated in *Longitudinal band analysis*). Each crosshair is a species with mean ± standard error. Positive temperature change means temperature distribution moving to the north, while negative means moving to the south. Positive northern range boundary change means species is consistent with expansion at the northern range limit, while negative means contraction. Species above the 1:1 line (gray dashed) suggest tracking temperature change.

Our results should not be interpreted to say that climate has no effect on species range limits. Sixty-two precent of species at nothern boundaries and 44% at southern boundaries are positively correlated with temperature change (Table A2). There is no relationship with precipitation change. Many variables affecting these boundaries could preclude the large geographic shifts needed to track climate. For example, adults might be controlled by annual mean temperature and precipitation, but offspring might be driven by temperature variabilities and extremes, growing season temperature or drought, spring precipitation, first-last day of frost, and so forth. Soils, disturbance, and land use change could provide a backdrop for species interactions, including competition, herbivore, and disease. If habitat destruction, degradation, and fragmentation resulted from land use change are proximate factors limiting response to climate (Hof *et al.*, 2011), vulnerability could shift from human effects in the near term to climate change in the near future.

Clark *et al.* (2003) emphasized that species range shifts cannot be predicted from seed dispersal characteristics and life history. The empirical evidence presented here should not be misinterpreted to say that seed characteristics have no impact. This study shows that most large-seeded species have patterns consistent with overall range contraction at both northern and southern range limits (Figure 1.5), a pattern that is suggestive of an effect, but different from the expected capacity to track warming at northern range limits. Like us, the meta-analysis of Angert *et al.* (2011) showed that seed mass and seed dispersal mode have low explanatory power for

range shifts of Swiss alpine plants. Crimmins *et al.* (2011) found that altitudinal range shifts of California plant species are unrelated to lifeform, physiognomy, dispersal mechanism, and fire adaptation. Such studies do not establish that seed traits are unimportant, because they are comparisons across rather than within species. Seed traits could have an impact on spread of many species without emerging as "significant" predictors of spread across species. The result that species-level traits do not correlate with migration potential suggests that use of seed size as an indicator of which species may track climate could be of limited utility.

1.4.4 Slow migration potential from models, experiments, and observational data

Model predictions that tree responses to climate change would be slow and unpredictable (Clark *et al.*, 2003) motivated an extensive seedling study to evaluate performance of residents and potential invaders (Ibanez *et al.*, 2008; Ibanez *et al.*, 2009). Invasion of new regions means that rare seeds traveling long-distances face competition from overwhelming numbers of locally produced seed. To overcome these odds, rare dispersers require local microsites where they are clearly superior to residents (Clark *et al.*, 2003), or locally disturbed sites, where local seed rain from potential competitors is low (Fastie, 1995). Models that make some effort to incorporate the many sources of uncertainty do not predict the rapid spread that comes from simple projection of dispersal kernels (Clark *et al.*, 2001; Clark *et al.*, 2003). Fourteen thousand seedlings of residents and potential invaders were planted and followed in competition for light and soil moisture, in gaps and in the forest understory, from southeastern Piedmont to northern hardwoods (Ibanez *et al.*, 2008; Ibanez *et al.*, 2009). Potential invaders consisted of species from warmer latitudes or elevations, likely to migrate north in response to contemporary climate change (Figure 1.1). Results showed no advantage to potential invaders, certainly not the dominance needed if they

were to overcome the numerical disadvantages required for rapid spread. Results of widespread seedling experiments on invasion (Ibanez *et al.*, 2008; Ibanez *et al.*, 2009) coupled with the FIA record of offspring-adult comparisons (this analysis) would appear to support model results that predict migration rates far below those required to track contemporary climate change.

2 Dual impacts of climate change: forest migration and turnover through life history

2.1 Introduction

Biogeographic responses of plants to climate change will be largely determined by the niche requirements of juveniles, which can limit the capacity of plant species to colonize new environments (Clark *et al.*, 2001; Ibanez *et al.*, 2008; Ibanez *et al.*, 2009). If juveniles and adults respond differently to climate variations, then niche models calibrated to adult distributions may provide limited guidance for species climate responses. This potential importance of juvenile requirements could be dismissed on the grounds that, where there are adults, there were once juveniles—adult distributions thus integrate effects of climate on both life stages. However, adults can be abundant as a result of climate trends or fluctuations that affected recruitment in the past (Agee, 1993; Clark, 1996). Because adult abundance accumulates the effects of past climate variation, models based on current climate-adult abundance might misrepresent the critical relationships between life history and climate. Incorporating juvenile distribution information together with that of adults could provide insight that directly relates to species response to climate change.

Ontogenetic shifts in species environmental requirements occur when organisms occupy different niches at different life history stages (Chase & Leibold, 2003). Despite a large literature on ontogenetic shifts in animals (reviewed by Werner & Gilliam, 1984), there is little direct evidence for how it affects migration potential of plants (Young *et al.*, 2005). Field experiments provide support for ontogenetic shifts in physiology (Parrish & Bazzaz, 1985; Donovan & Ehleringer, 1991; Cavender-Bares & Bazzaz, 2000; Thomas & Winner, 2002; Bansal & Germino, 2010; Kulmatiski & Beard, 2012), demography (Poorter, 1999; Eriksson, 2002; Miriti,

2006; Warren & Bradford, 2011), phenology (Yang & Rudolf, 2010), and functional traits (Butterfield & Briggs, 2011; Herault *et al.*, 2011; Houter & Pons, 2012; Palow *et al.*, 2012), but few studies investigate biogeographic responses (Stohlgren *et al.*, 1998; Quero *et al.*, 2008; Bertrand *et al.*, 2011; Urbieta *et al.*, 2011). For tree species, seedlings and adult trees are usually not part of the same analysis. Previous studies concentrate on either trees greater than a minimum diameter (e.g., Iverson & Prasad, 1998; Canham & Thomas, 2010) or on seedlings (e.g., Ibanez *et al.*, 2008; Ibanez *et al.*, 2009). Thus, there is little opportunity to directly compare responses of large and small trees and to infer ontogenetic shifts.

Species distribution models (SDMs) are the main tool used to study climate change impacts on forest biodiversity at regional scales (Botkin *et al.*, 2007; Elith & Leathwick, 2009; McMahon *et al.*, 2011; Bellard *et al.*, 2012), yet few consider responses from both juvenile and adult trees (Bykova *et al.*, 2012). One of the fundamental assumptions for SDMs is that species niches are retained over time, i.e., niche conservatism (Wiens & Graham, 2005; Pearman *et al.*, 2008; Wiens *et al.*, 2010; Peterson, 2011). Niche conservatism has been studied in the context of species invasion (Broennimann *et al.*, 2007; Beaumont *et al.*, 2009; Gallagher *et al.*, 2010; Petitpierre *et al.*, 2012) and evolution (Maiorano *et al.*, 2012), but not at different life history stages. The notion of niche conservatism leads to the prediction that species will shift their ranges poleward in latitude and upward in elevation in response to climate warming, a pattern that is evident for some species in some regions (Walther *et al.*, 2005; Beckage *et al.*, 2008; Kelly & Goulden, 2008; Lenoir *et al.*, 2008; Gottfried *et al.*, 2012; Pauli *et al.*, 2012).

In the eastern United States, the northern range limits of most tree species appear to be stable through time, which is contrary to the predictions of SDMs under climate change (Iverson & Prasad, 1998; McKenney *et al.*, 2007). Among the few empirical studies on latitudinal tree

migration, Woodall *et al.* (2009) found that juveniles have higher mean latitudes than adults for northern species, suggesting northward range shifts, but not for southern species. They recognized that all their northern species have distributions that are truncated at the US-Canada border, so the use of mean latitude might not reflect species actual distributions. By comparing range edge distributions of juveniles vs. adults, Zhu *et al.* (2012) found that there is not yet evidence for latitudinal migration for more than half of the 92 tree species analyzed in eastern US forests. More recently, Woodall *et al.* (2013) combined the juvenile-adult geographic analysis with forest disturbance metrics, and confirmed the stability of tree northern range margins. All these empirical juvenile-adult analyses in geographic space suggest that large-scale tree northward migration, especially along northern range margins, has not yet occurred. A more mechanistic understanding of why responses may be slow requires new approaches to the effects of climate on adults and juveniles (Jackson *et al.*, 2009). Therefore, we propose to extend the geographic comparison into climate space.

In this analysis, we investigate how juveniles and adult trees differ in their relationships with regional climate variation, focusing on two hypotheses. Recognizing that adult distributions represent recruitment of the past, latitudinal migration suggests that juveniles will be more concentrated in cold climates than adults—these are areas warm enough for contemporary colonization that were not previously suitable when mature individuals became established. Alternatively, if species are not migrating, then we might observe juveniles concentrated in warm climates simply because higher temperature implies higher turnover rate. The rationale is based on the observation that growth is promoted by long growing seasons, and rapid growth increases competition and mortality rates (Assmann, 1970; Clark, 1990). Specifically, we evaluate the following two hypotheses:

1. *Migration hypothesis.*—A population migrating northward in response to a warming climate will have juveniles located further north than adults. When mapped in climate space, juveniles would be relatively more abundant than adults in cold and dry climates, as low temperature is usually associated with low precipitation because of high correlation. Driven by constant climate-distribution relationships and future climate scenarios, northward shift in habitat is one of the predictions of SDMs based on distribution and abundance data from adults (Iverson & Prasad, 1998; McKenney *et al.*, 2007; Iverson *et al.*, 2008). By incorporating juvenile distribution and abundance, we can compare the difference between juveniles and adults in climate space and geographic space.
2. *Turnover hypothesis.*—Increasing temperature and precipitation could increase turnover rates, i.e., rapid growth, increased mortality, and elevated recruitment. The most obvious cause for this phenomenon is a prolonged growing season, but it could also result if growth increases with temperature and precipitation during the growing season. The latter occurs if individuals are below their temperature optima and they are not limited by drought or other factors. Juveniles could be relatively more abundant than adults in warm and wet climates if increased mortality increases recruitment opportunities. Higher turnover in warm and wet climate is suggested by a legacy of physiological experiments (Saxe *et al.*, 2001), a global meta-analysis on population dynamics across latitude and elevation (Stephenson & van Mantgem, 2005), and long-term demographic observations in tropical forests (Phillips & Gentry, 1994; Phillips *et al.*, 2004). This prediction of high recruitment, and thus

high turnover, in warm and wet climates is contrary to the pattern expected by northward migration hypothesis—recruitment shifted to higher latitudes than adults.

In this study, we evaluate one of the most extensive sources of biogeographic information on juvenile and adult tree species to quantify climate differences through life history and consider its role for potential change. We make use of species abundance data from the Forest Inventory and Analysis (FIA) program of the USDA Forest Service, with millions of tree observations and a consistent sampling scheme for a continuum of size classes. We adopt the usual assumption that species distributions in geographic space correspond to the realized niches in climate space, recognizing that those relationships are influenced by interactions with other species (Pulliam, 2000; Soberon & Nakamura, 2009; Peterson *et al.*, 2011; Wiens, 2011). Our modeling strategy differs from previous approaches in which we jointly analyze juveniles and adults to understand the interactions that contribute to distributions at biogeographic scale. We compare the abundance-climate response surfaces between juveniles and adults for each species, and synthesize overall patterns among all species.

2.2 Materials and methods

We combined forest inventory and climate data to construct a joint SDM, and we compared juvenile vs. adult abundance in climate space. First, we aggregated data to regional scales to understand species biogeographic responses to climate. Instead of modeling all observations, we focused on nonzero observations where species are present, because we were interested in whether or not abundance within the range varies along climate gradients, and previous analysis of occurrence (zeros and nonzeros) did not provide evidence that populations are migrating in response to climate change. To test the migration and turnover hypotheses, we directly compared the optimal climate conditions for juveniles and adults. We then calculated the

ratio of juvenile to adult abundance, i.e., relative recruitment intensity, in climate space. Finally, we synthesized results across species to a relative recruitment score by standardizing relative recruitment intensity of each species.

2.2.1 Forest inventory data

The FIA program is the primary source for information about the extent, condition, status, and trends of forest resources in the United States (Smith *et al.*, 2009). FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships across the United States, resulting in national sample intensity of one plot per 2,428 ha (Bechtold & Patterson, 2005). Classified satellite imagery is used to stratify sampling. Forested land is defined as areas with at least 10% covered by tree species canopies, at least 0.4 ha in size, and at least 36.6 m wide. FIA inventory plots consist of four, 7.2 m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Bechtold & Patterson, 2005). All trees (standing live and dead) with a diameter at breast height (DBH) of at least 12.7 cm are inventoried on forested subplots. Within each subplot, a 2.07 m radius microplot offset 3.66 m from subplot center is established where only live trees with a DBH between 2.5 and 12.7 cm are inventoried. Within each microplot, all live tree seedlings are tallied according to species. Conifer seedlings must be at least 15.2 cm in height with a root collar diameter less than 2.5 cm. Hardwood seedlings must be at least 30.5 cm in height with a root collar diameter less than 2.5 cm. Note that they are often well established stems, typically not 1st-yr seedlings.

In this analysis, FIA data were extracted from the recent annual inventories (1999 to 2008) in 31 eastern states for a total of 43,396 inventory plots from FIADB version 4.0 on March 16, 2010 (available online http://fia.fs.fed.us/). Because we were interested in tree species abundance within their respective ranges in climate space, we focused on species with substantial

sample sizes in the eastern United States. We used the species list from Iverson and Prasad (1998) to further restrict analysis to 65 species, by excluding genus-level species and riparian/hydric species (Table B1 includes the complete species list). These 65 common species span major plant functional types in North America. To compare species abundance in different life stages, we followed the FIA sampling design to divide the data into two size classes: (i) seedling (DBH < 2.54 cm), and (ii) tree (DBH ≥ 2.54 cm). For each species, we extracted the seedling count and tree basal area in each plot. The condition delineation in FIA database was used to identify fully forested, non-plantation plots that have both seedling and tree surveys.

2.2.2 Climate and ecoregion data

Climate data in this study were extracted from the 800 m resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) data set (available online http://prism.nacse.org/). Recognized as a high quality spatial climate data set in the United States, PRISM is an interpolation of meteorological station data to produce continuous, digital grid estimates of climatic parameters, with consideration of location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly *et al.*, 2008). We used long-term average climate data (1990 to 2010) corresponding to each FIA plot as the climate covariates. We extracted annual mean temperature (˚C), ranging from 0 ˚C to 25 ˚C, and annual precipitation (mm), ranging from 550 mm to 1,650 mm. We used these two variables because they are important to species distributions (Peterson *et al.*, 2011), commonly used in SDMs (Elith & Leathwick, 2009), and are highly correlated with other climate variables.

Since the actual FIA plot coordinates are not publicly available, the longitude and latitude of plot locations have been perturbed in an unbiased direction not exceeding 1.67 km, and

typically within a 0.8 km radius of the actual plot location, so as to facilitate study repeatability without introducing bias (McRoberts *et al.*, 2005). The spatial resolution of PRISM data is similar to that of the FIA perturbed plot locations. We therefore used the publicly available perturbed plot coordinates to match the FIA plot location with the PRISM climate data.

We performed our analysis at an aggregated regional scale, not at the individual FIA plot scale, because regional climate and local species abundance data are misaligned. Tree abundance varies along climate gradients at regional scales (Iverson & Prasad, 1998), but not at plot scales (Canham & Thomas, 2010). This incongruity is expected due to the fact that regional climate data are not resolved at the plot scale, but microclimate, drainage, and competition vary locally. Therefore, we followed an alternative option similar to that of Iverson and Prasad (1998) to aggregate plot-level FIA data to a scale more compatible with regional climate data. The ecological subsection (hereafter *ecoregion*) is essentially a collection of plots where each unit defines a region of unique ecological characteristics of surficial geology, lithology, geomorphic process, soil groups, subregional climate, and potential natural communities that differs from neighboring units in the United States (Cleland *et al.*, 1997; Keys *et al.*, 2007; McNab *et al.*, 2007). In our study area of the eastern United States, we aggregated the plot-level data (n = 43,396) into the ecoregion-level data (n = 427) by averaging seedling densities (#/ha), tree basal areas ($m^2\ ha^{-1}$), annual mean temperature (˚C), and annual precipitation (mm) of plots within each ecoregion.

2.2.3 Species distribution model

We adopted the framework from S. Ghosh, K. Zhu, A.E. Gelfand & J.S. Clark (unpublished data) to jointly model seedling densities as juvenile response and tree basal areas (BAs) as adult response, based on the rationale that tree BAs depend on climate, and seedling

densities depend on both climate and tree BAs through reproduction. Tree BAs could affect seedling densities through both reproduction (a positive effect) and competition (shading, a negative effect). We constructed a SDM for ecoregions using plots with nonzero seedling densities and tree BAs. At the ecoregion scale, a zero observation indicates absence from all 100 seedling and tree plots located in a geographic area over 7,000 km^2. The SDM is constructed and fitted in a Bayesian framework to allow interdependence and coherent inference.

In ecoregion i, we modeled the tree BA (Z_i) as a lognormal distribution with mean linked to climate,

$$\begin{aligned} Z_i &\sim \text{Lognormal}\left(\mu_i, \sigma^2\right) \\ \mu_i &= X_i \alpha \end{aligned} \qquad 4$$

where $X_i = \left[1, T_i, P_i, T_i^2, P_i^2, T_i P_i\right]$ is the climate design matrix (temperature T_i and precipitation P_i), with $\alpha = \left[\alpha_0, \alpha_1, \alpha_2, \alpha_3, \alpha_4, \alpha_5\right]^{\mathrm{T}}$ as the climate coefficients. Likewise, we modeled the seedling density (Y_i) as a lognormal distribution with mean linked to climate and tree BA (Z_i) in the corresponding ecoregion i,

$$\begin{aligned} Y_i &\sim \text{Lognormal}\left(\lambda_i, \delta^2\right) \\ \lambda_i &= X_i \beta + Z_i \gamma \end{aligned} \qquad 5$$

where the climate design matrix (X_i) is the same as in Equation 4, with $\beta = \left[\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5\right]^{\mathrm{T}}$ as the climate coefficients, and γ as the coefficient linking seedling density to tree BA.

We used the standard semi-conjugate non-informative priors on $\alpha, \beta, \gamma \sim \text{Normal}\left(0, 10^2\right)$ and $\sigma^2, \delta^2 \sim \text{InvGamma}\left(0.05, 0.05\right)$. Climate covariates were centered and scaled to unit standard deviation. Implemented in the full Bayesian framework, parameter posterior distributions were simulated using Markov chain Monte Carlo (MCMC). Convergence was checked by both visually assessing trace plots and Geweke diagnostics after 100,000 iterations for each species.

To compare the ecoregion-level and plot-level models, we implemented the same SDM to data at both scales. We checked model performance using in-sample predictions by composite sampling from Equations 4 and 5. We summarized model fit by goodness-of-fit measures, R_Y^2 for seedling density and R_Z^2 for tree BA,

$$R_Y^2 = 1 - \frac{\sum_i \left(Y_i - \hat{Y}_i\right)^2}{\sum_i \left(Y_i - \overline{Y}\right)^2}$$
$$R_Z^2 = 1 - \frac{\sum_i \left(Z_i - \hat{Z}_i\right)^2}{\sum_i \left(Z_i - \overline{Z}\right)^2} \qquad 6$$

where Y_i and Z_i are observed seedling density and tree BA, $\hat{Y}_i$ and $\hat{Z}_i$ are predicted seedling density and tree BA in ecoregion/plot *i*, $\overline{Y}$ and $\overline{Z}$ are average observed seedling density and tree BA. Both R_Y^2 and R_Z^2 range from 0 to 1, with greater values indicating better model fit.

2.2.4 Response surface comparisons

We used the fitted SDM to predict species abundance in a gridded climate space ($T \times P$) as species response surfaces. In other words, a species has predicted seedling densities (#/ha) and

tree BAs (m^2 ha^{-1}) within its geographic range mapped in the climate space of annual mean temperature (˚C) and annual precipitation (mm). To compare the difference of seedling vs. tree response surfaces, we first calculated the optimal climate conditions as the temperature and precipitation weighed by the predicted abundances. For seedling response surfaces, the optimal temperature ($\tilde{T}_Y$) and precipitation ($\tilde{P}_Y$) are

$$\tilde{T}_Y = \frac{\sum_j \hat{Y}_j T_j}{\sum_j \hat{Y}_j}$$
$$\tilde{P}_Y = \frac{\sum_j \hat{Y}_j P_j}{\sum_j \hat{Y}_j} \quad (7)$$

where $\hat{Y}_j$ is the predicted seedling density (#/ha) in climate grid *j*, with annual mean temperature T_j (˚C) and annual precipitation P_j (mm). Likewise, for tree response surfaces, the optimal temperature ($\tilde{T}_Z$) and precipitation ($\tilde{P}_Z$) are

$$\tilde{T}_Z = \frac{\sum_j \hat{Z}_j T_j}{\sum_j \hat{Z}_j}$$
$$\tilde{P}_Z = \frac{\sum_j \hat{Z}_j P_j}{\sum_j \hat{Z}_j} \quad (8)$$

where $\hat{Z}_j$ is the predicted tree BA (m^2 ha^{-1}) in climate grid *j*, with annual mean temperature T_j (˚C) and annual precipitation P_j (mm). Ontogenetic niche shifts are suggested by the differences in the optimal climate conditions between seedling and tree response surfaces. For each species, the migration hypothesis is supported if the seedling surface has lower optimal temperature

and/or precipitation than the tree surface ($\tilde{T}_Y < \tilde{T}_Z$ and/or $\tilde{P}_Y < \tilde{P}_Z$). In contrast, the turnover hypothesis is supported if the seedling surface has higher optimal temperature and/or precipitation than the tree surface ($\tilde{T}_Y > \tilde{T}_Z$ and/or $\tilde{P}_Y > \tilde{P}_Z$).

To identify the climate conditions that relatively benefit seedlings over trees, we then calculated the relative recruitment intensity (R_j) in climate space,

$$R_j = \frac{\hat{Y}_j}{\hat{Z}_j} \tag{9}$$

where $\hat{Y}_j$ is the predicted seedling density (#/ha), $\hat{Z}_j$ is the predicted tree BA ($m^2\ ha^{-1}$) in climate grid *j*. Relative recruitment intensity (R_j, $\#/m^2$) is large in climate conditions where seedling abundance is relatively higher than tree abundance. For each species, the migration hypothesis is supported if its relative recruitment intensity is high in cold and dry climates. In contrast, the turnover hypothesis is supported if its relative recruitment intensity is high in warm and wet climates. This index (R_j) in the entire climate space gives more comprehensive understanding than the optimal temperature ($\tilde{T}_Z$) and precipitation ($\tilde{P}_Z$) summaries of the seedling and tree response surfaces.

To summarize the differences of seedling vs. tree response surfaces, we finally calculated a standardized score for all 65 species. For each species, the relative recruitment intensity (R_j) was standardized by subtracting its mean and dividing by its standard deviation (sd),

$$\tilde{R}_{jk} = \frac{R_{jk} - \text{mean}_j\left(R_{jk}\right)}{\text{sd}_j\left(R_{jk}\right)} \tag{10}$$

where $\tilde{R}_{jk}$ is the standardized relative recruitment intensity (unitless) in climate grid *j*, for species *k*. This index is comparable among species after standardization (Equation 10). It was then averaged across species to obtain the relative recruitment score (S_j),

$$S_j = \text{mean}_k \left(\tilde{R}_{jk} \right) \quad 11$$

in climate grid *j*, for species *k*. A higher score (S_j, unitless) identifies climate conditions where seedlings are relatively more abundant than trees. Across all species, the migration hypothesis is supported if the relative recruitment score is high in cold and dry climates. In contrast, the turnover hypothesis is supported if the relative recruitment score is high in warm and wet climates. This score in the entire climate space summarizes seedling and tree response surfaces for all species.

All analyses were performed in R version 2.15.0 (R Development Core Team, 2012).

2.3 Results

For each species, our SDM predicts seedling and tree abundance at the ecoregion scale, but not at the plot scale. We checked model fit using in-sample prediction for seedling densities and tree BAs at two scales, and we summarized model fit using the goodness-of-fit measures (Equation 6). As an example species, *Pinus taeda* (loblolly pine) seedling and tree abundances within its range are well predicted by the model at the ecoregion scale (Figure 2.1a and b), with goodness-of-fit $R_Y^2 = 0.77$ for seedlings and $R_Z^2 = 0.51$ for trees. However, the same model has no predictive capacity at the plot scale (Figure 2.1c and d), with goodness-of-fit $R_Y^2 = 0.0017$ for seedlings and $R_Z^2 = 0.0013$ for trees. This pattern—that climate can predict abundance at the

ecoregion but not at the plot scale—is true for all 65 species (Table B1). This result does not mean that seedling densities and tree BAs are unresponsive at the plot scale; rather climate data are misaligned, being smoothed at geographic scales much coarser than individual plots, and there are additional local variables that affect plot-level data. The ecoregion-level model aggregates FIA data at a scale that is in closer alignment with climate. Hereafter, we focus on results from the ecoregion-level models.

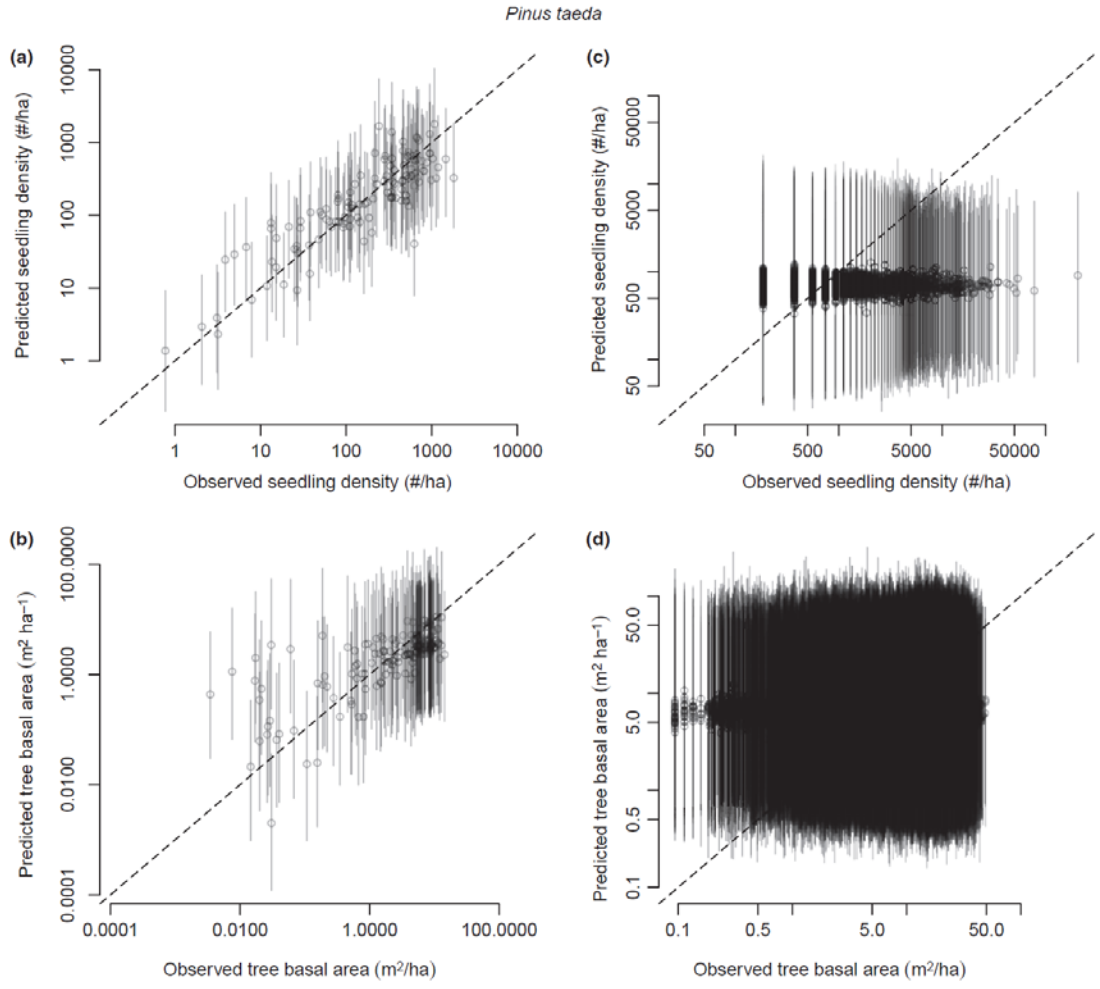

Figure 2.1: Model checking (in-sample prediction) of an example species, *Pinus taeda*, at ecoregion (a, b) vs. plot scale (c, d). Points and solid lines are posterior predictive means and 95% credible intervals, and dashed lines are the 1:1 reference. The ecoregion-

level model performs significantly better than the plot-level model for both seedling density (a vs. c) and tree basal area (b vs. d), because regional climate and plot-level species abundance are spatially misaligned. All the subsequent figures are results from the ecoregion-level model.

At the ecoregion scale, the fitted SDM predicts change in species abundance along climate gradients. For example, *Pinus taeda* seedling density and tree BA are both abundant in warm (15 – 20 ˚C annual mean temperature) and wet (1,400 – 1,600 mm annual precipitation) climates (surfaces in Figure 2.2a and b). The optimal climates for the seedling response surface (Equation 7) are $\tilde{T}_Y = 19.30\,^{\circ}\mathrm{C}$ and $\tilde{P}_Y = 1530\,\mathrm{mm}$. The optimal climates for the tree response surface (Equation 8) are $\tilde{T}_Z = 18.80\,^{\circ}\mathrm{C}$ and $\tilde{P}_Z = 1460\,\mathrm{mm}$. In this case, the turnover hypothesis is supported because the seedling surface has higher optimal temperature ($\tilde{T}_Y > \tilde{T}_Z$) and precipitation ($\tilde{P}_Y > \tilde{P}_Z$) than the tree surface. The relative recruitment intensity, i.e., ratio of seedling density vs. tree BA (Equation 9), indicates that seedling recruitment is more concentrated in warm and wet climates than adult abundance (Figure 2.2c). This result does not mean that cold and dry climates are detrimental for either seedlings or trees; rather it demonstrates how recruitment varies with climate relative to adult abundance. This trend in relative recruitment intensity is consistent with the hypothesis that warm and wet climates have high population turnover. It is inconsistent with northward migration.

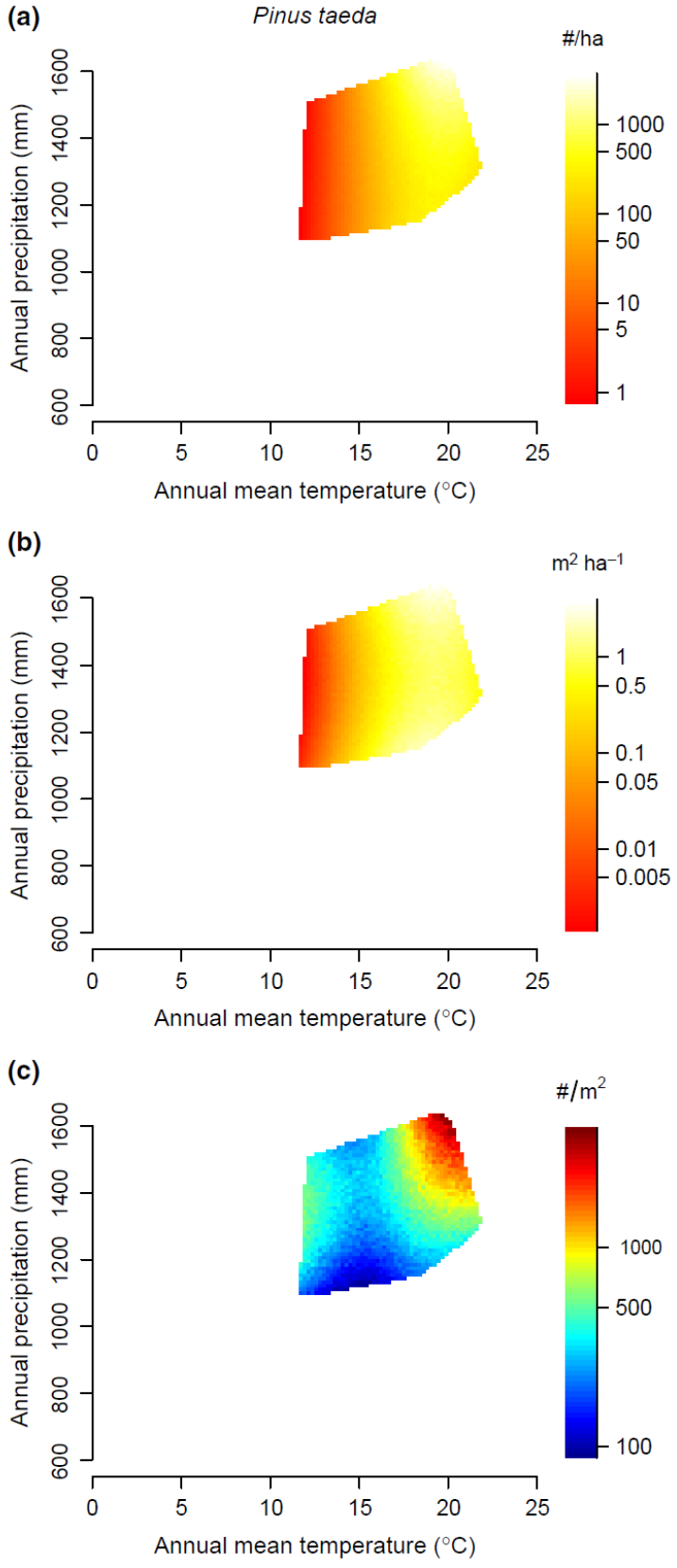
(a)
Pinus taeda
#/ha
1000
500
100
50
10
5
1
Annual precipitation (mm)
600
800
1000
1200
1400
1600
0
5
10
15
20
25
Annual mean temperature (°C)
(b)
m² ha⁻¹
1
0.5
0.1
0.05
0.01
0.005
Annual precipitation (mm)
Annual mean temperature (°C)
(c)
#/m²
1000
500
100
Annual precipitation (mm)
Annual mean temperature (°C)

Figure 2.2: Abundance response surfaces for seedling density (a), tree basal area (b), relative recruitment intensity (c) from the fitted ecoregion-level model of an example species, *Pinus taeda*. Abundance response surfaces of seedlings (a) and trees (b) show clear patterns within species range (colored images) in the climate space (annual mean temperature and annual precipitation). Relative recruitment intensity (c), calculated as the ratio of (a) over (b), as in Equation 9, identifies the climate conditions that relatively benefit seedlings over trees. In this case, warm and wet climates benefit *Pinus taeda* recruitment.

An alternative example is *Ilex opaca* (American holly) with both seedlings and trees being abundant in moderate (15 ˚C annual mean temperature and 1,400 mm annual precipitation) climates (surfaces in Figure 2.3a and b). The optimal climates for the seedling response surface (Equation 7) are $\tilde{T}_Y = 16.20\,^{\circ}\text{C}$ and $\tilde{P}_Y = 1340\,\text{mm}$. The optimal climates for the tree response surface (Equation 8) are $\tilde{T}_Z = 17.50\,^{\circ}\text{C}$ and $\tilde{P}_Z = 1480\,\text{mm}$. In this case, the migration hypothesis is supported because the seedling surface has lower optimal temperature ($\tilde{T}_Y < \tilde{T}_Z$) and precipitation ($\tilde{P}_Y < \tilde{P}_Z$) than the tree surface. The relative recruitment intensity (Equation 9) is concentrated in cold climates (Figure 2.3c). This trend appears to suggest northward migration for this species.

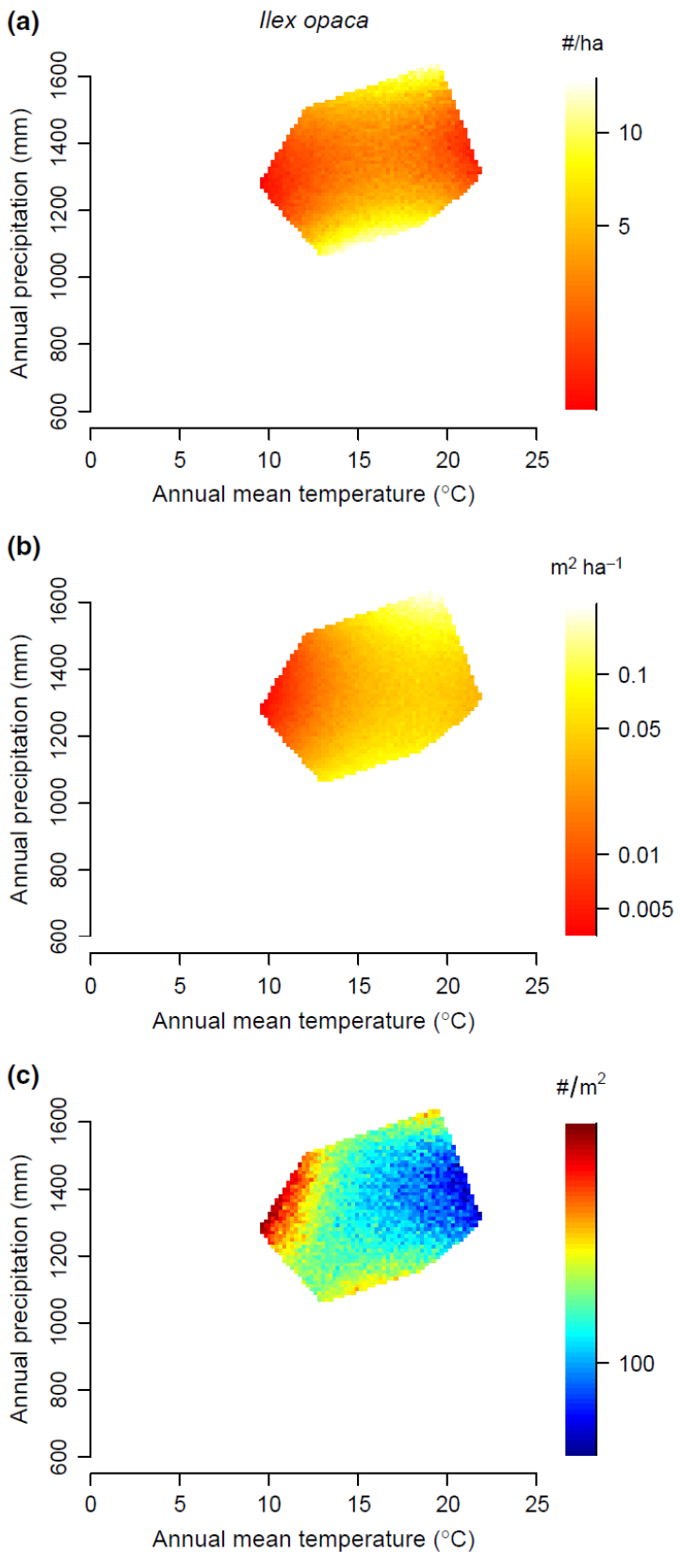
(a)
Ilex opaca
#/ha
10
5
Annual precipitation (mm)
600
800
1000
1200
1400
1600
0
5
10
15
20
25
Annual mean temperature (°C)
(b)
m² ha⁻¹
0.1
0.05
0.01
0.005
Annual precipitation (mm)
Annual mean temperature (°C)
(c)
#/m²
100
Annual precipitation (mm)
Annual mean temperature (°C)

Figure 2.3: Abundance response surfaces for seedling density (a), tree basal area (b), relative recruitment intensity (c) from the fitted ecoregion-level model of an example species, *Ilex opaca*. Symbolism follows Figure 2.2. In this case, cold climates benefit *Ilex opaca* recruitment.

Taken across all species, the turnover hypothesis is predominately supported by the optimal temperature and precipitation comparisons between seedling and tree response surfaces. For optimal temperature, 50 out of 65 species (77%) support the turnover hypothesis ($\tilde{T}_Y > \tilde{T}_Z$), but only 15 out of 65 species (23%) support the migration hypothesis ($\tilde{T}_Y < \tilde{T}_Z$). For optimal precipitation, 54 out of 65 species (83%) support the turnover hypothesis ($\tilde{P}_Y > \tilde{P}_Z$), but only 11 out of 65 species (17%) support the migration hypothesis ($\tilde{P}_Y < \tilde{P}_Z$). The differences between seedling and tree surfaces are also consistent with ontogenetic niche shifts in species climate-abundance relationships, indicating seedlings and trees respond differently to this regional climate variation. We include the optimal climates and supports for migration or turnover hypothesis for each species in Table B1.

Synthesized over all species, the turnover hypothesis is supported by patterns in the relative recruitment score, where warm and wet climates have relatively higher seedling than tree abundance (Figure 2.4). The relative recruitment score is a standardized summary of relative recruitment intensity for all 65 species (Equations 10 and 11). It offers an alternative perspective from the individual view of the optimal climates (Equations 7 and 8). Across 65 species, the climates that benefit most seedlings than trees are roughly at 20 ˚C annual mean temperature and 1,500 mm annual precipitation. In contrast, temperatures below 10 ˚C generally have relatively low seedling than tree abundance. In summary, the turnover hypothesis is supported by the majority of individual species (optimal climates, Table B1) and by the synthesis across species (relative recruitment score, Figure 2.4).

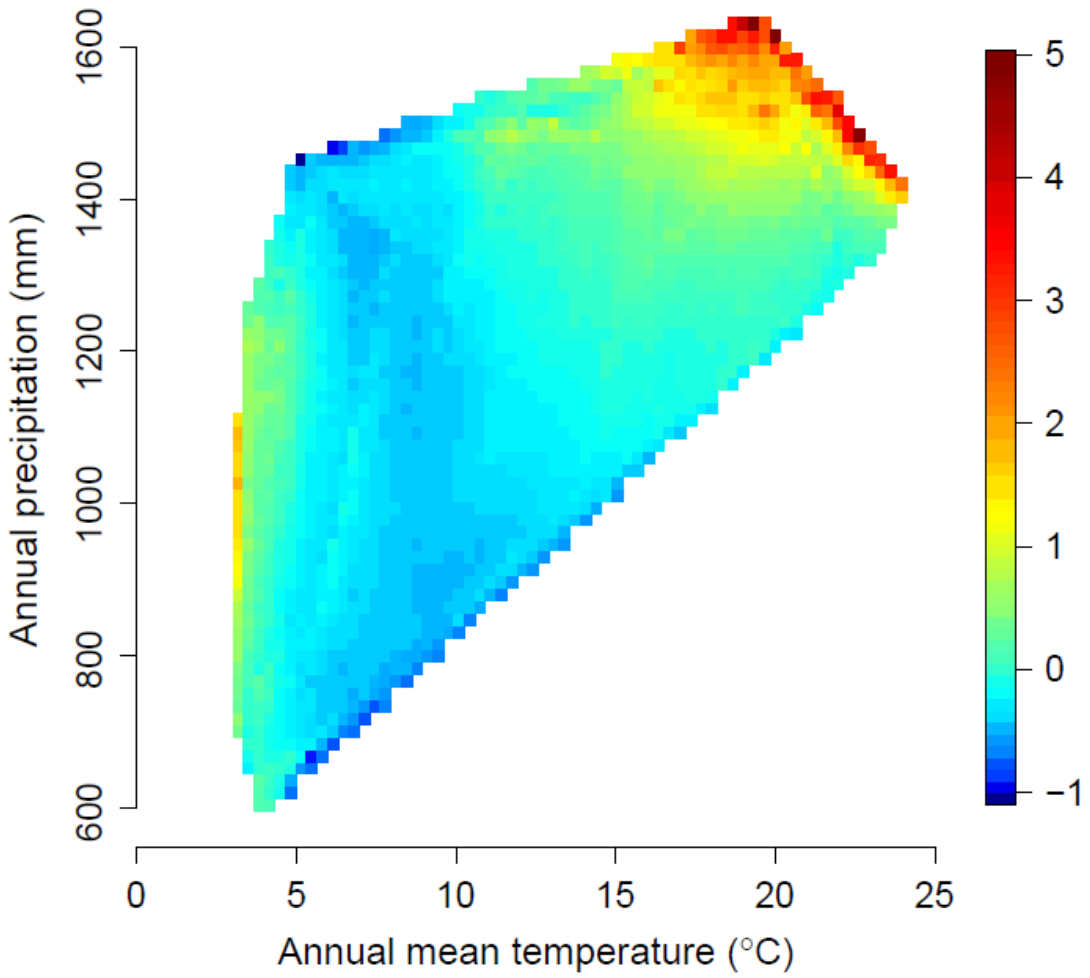

Figure 2.4: Relative recruitment score from the fitted ecoregion-level models across all 65 species. Relative recruitment score is calculated as the species average of standardized relative recruitment intensity, as in Equations 10 and 11. On average, warm and wet climates benefit species recruitment.

2.4 Discussion

By comparing juvenile vs. adult tree abundance in climate space, we found that regional-scale recruitment across species is relatively more abundant in warm and wet climates in the eastern United States. Distributions of juveniles vs. adults differ in ways that are more consistent with geographic trends in turnover but less with migration in response to climate change. These

results are consistent with the previous geographic analysis of range limits, which did not show evidence of large-scale latitudinal migration either (Zhu *et al.*, 2012). High turnover in warm and wet climates per se does not mean that populations are threatened by climate warming. Rather, it is consistent with the effects of more rapid dynamics that are possible when growing seasons are long, resulting in faster maturation, more rapid thinning, and elevated recruitment. However, failure to migrate is a clear concern in the face of rapid climate change. For some species, the differences between juveniles and adults suggest ontogenetic shifts in species climatic requirements, which challenge the assumption of niche conservatism through life history. In addition, we identified several key issues in modeling species distributions including local vs. regional scales and zero abundance observations.

2.4.1 Forest responses to climate change

The turnover hypothesis is supported by the fact that relative recruitment dominates in warm and wet climates both for the majority of individual species (Table B1) and the synthesis of all species (Figure 2.4). Most species (~ 80%) show patterns like *Pinus taeda*, having higher optimal temperature and/or precipitation for juveniles than adults, and few (~ 20%) show patterns like *Ilex opaca*, having lower optimal temperature and/or precipitation for juveniles than adults (Table B1). Results of these two example species are consistent with the geographic analysis at local scales that indicates *Ilex opaca* has a tendency of northward migration (figure 4a and b, and table S1 in Zhu *et al.*, 2012), but *Pinus taeda* does not (table S1 in Zhu *et al.*, 2012). Among all these common eastern US species, the turnover hypothesis is supported by many genera (*Acer* spp., *Betula* spp., *Carya* spp., *Pinus* spp., *Quercus* spp., *Ulmus* spp.) and species (*Carpinus caroliniana*, *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Ostrya virginiana*). Furthermore, the relative recruitment score, a standardized metric of juvenile-

adult abundance ratio for all species, also suggests that warm and wet climates have relatively high recruitment (Figure 2.4). In this case, the turnover hypothesis applies to not only individual species, but also total recruitment. If dynamics are accelerated in warm or wet regions, the species that benefit will change with the overall change in turnover. We do not expect recruitment of all species to increase uniformly, but we do expect that overall growth, mortality, and recruitment will increase.

Faster tree population turnover in warm and wet climates is supported by a range of theoretical, experimental, and observational studies. Theory predicts that rapid tree growth results in thinning and turnover (Clark, 1991), which is promoted by fertility, growing season length, and moisture. Experiments at boreal and temperate latitudes show that rising temperatures affect all major chemical and biological processes that can influence forest dynamics, including photosynthesis, respiration, soil nutrient availability, and ontogenetic development (Saxe *et al.*, 2001). A synthesis of observations from many sites across the globe consistently supports higher recruitment and mortality rates in tropical than temperate forests and declining turnover with elevation, i.e., a proxy of temperature (Stephenson & van Mantgem, 2005). Long-term monitoring in tropical forests reveals increasing tree population turnover rates through time (Phillips & Gentry, 1994; Lewis *et al.*, 2004b; Phillips *et al.*, 2004), but the global change agents have not yet been identified because the data are sparse both spatially and temporally (Lewis *et al.*, 2004a). The massive, consistently-sampled temperate forest inventory data set available for this analysis provides clear evidence that relative recruitment rates increase with geographic gradients in temperature and precipitation.

The juvenile-adult comparison in geographic space (Zhu *et al.*, 2012) and climate space (this analysis) both show that large-scale poleward tree migration is not yet evident even in a data

set as exhaustive as FIA. In geographic space, a poleward migration would be characterized by juveniles that are shifted to the north of adults. On the contrary, we found that most species are not experiencing northward migration at their northern range limits (i.e., high latitudes) where temperatures have increased most during the 20th century (figure 6 in Zhu *et al.*, 2012). In climate space, the migration hypothesis predicts that juveniles would be more abundant than adults in cold and dry climates. Here we demonstrate that patterns of juveniles and adults are inconsistent with a climatically driven migration signal. Instead, we found that recruitment is relatively more abundant in warm and wet climates. Insights gained from climate envelope projections of large-scale northward shift in habitat (Iverson & Prasad, 1998; McKenney *et al.*, 2007; Iverson *et al.*, 2008) could be updated with this evidence from juvenile-adult relationships.

Our comparisons between juvenile and adult responses show markedly different abundance-climate relationships through life history. Apparent regional-scale ontogenetic shifts in climatic requirements from this FIA analysis is consistent with plot-scale observations (Harper & White, 1974; Grubb, 1977). The difference between juvenile and adult responses challenges the assumption of niche conservatism through life history stages. As one of the pivotal assumptions of SDMs, niche conservatism suggests that species niches are retained over time. In a biogeographic setting like ours, species realized niches are approximated by distribution-environment relationships (Peterson *et al.*, 2011). Our relative recruitment intensities indicate that the regeneration niche can look different from those of adults even when observed at the regional scale. Transplant experiments also suggest that adult abundance might provide a poor indication of the niche requirements, and cast doubt upon SDMs based solely on adult distribution data (Warren & Bradford, 2011). Among the factors that can produce these life history differences are strong interactions between climate and competition, which differs for seedlings and adult trees.

Clark *et al.* (2011b) found that the effects of both temperature and drought interact with light and local moisture availability. Because seedlings of most species are subject to lower light levels, these interactions provide reasons to expect a shift in the climate impacts with age. These results highlight the importance of recognizing differences between juveniles and adults in biogeographic studies (McLaughlin & Zavaleta, 2012; Mok *et al.*, 2012; Bell *et al.*, 2014).

We recognize some of the important caveats that can influence interpretation of these relationships. In addition to climate, differences between distributions of juveniles and adults can result from regional-scale patterns in succession. We have not found differences between early vs. late successional species in our results (Table B1), and our aggregation from plots to ecoregions also reduces the influence of successional trends. However, we feel that this issue must still be considered in the future. Land use legacies could play a role. To minimize its effects, we only included FIA plots that are natural (non-plantation) and fully forested. However, there is still a strong tendency toward stands of a limited age range, dating from 19th century reforestation in the eastern United States. Note that source-sink population dynamics is not an important consideration in this analysis, because we focused on regional-scale, not local-scale, species abundance-climate relationships. Finally, relative recruitment scores at the edge of the climate space (Figure 2.4) should be interpreted with caution, because evidence is weakest there.

2.4.2 Regional species distribution modeling

We found that models fitted at the ecoregion scale predict abundance, but those fitted at the plot scale do not (Figure 2.1 and Table B1). Others have noted lack of predictive capacity from models at this scale and interpret it as lack of response (Canham & Thomas, 2010). Iverson and Prasad (1998) resolved the misalignment between plot data and smoothly varying climate by county-level aggregation (~ 100,000 ha). Likewise, Boucher-Lalonde *et al.* (2012) found that a

single, simple model could predict North American tree occurrence in climate space at a coarse scale (~ 40,000 ha). Apparent contradiction results from spatial misalignment of coarse scale climate and fine scale tree data. Biogeographic responses are not limited to coarse spatial scales; they are simply not available from aggregated data.

The scale alignment of individual- and aggregated-level data has been recognized as a widespread and oft-ignored phenomenon termed the *ecological fallacy* or *Simpson's paradox*. It often leads to confusing and even paradoxical interpretations of ecological data (Clark *et al.*, 2011a). In the context of species distribution modeling, it can occur when regional temperature and precipitation data do not capture local microclimate relationships that result from drainage, slope, aspect, albedo, wind fields, etc. If climate data are spatially smoothed and interpolated, then those data can be most productively applied to species distribution data aggregated at a similar scale.

The misalignment problem is especially relevant for spatial data at biogeographic scales, and it has long been recognized by statisticians (Banerjee *et al.*, 2004) and geographers (Scott *et al.*, 2002). Analyses with SDMs often take particular care with the scale of data (Hallett *et al.*, 2004; Pearson *et al.*, 2004; Diez & Pulliam, 2007; Trivedi *et al.*, 2008; Randin *et al.*, 2009; Seo *et al.*, 2009; McGill, 2010; Franklin *et al.*, 2012). In our context, species abundance and distribution are aggregations of individual demographic and physiological performance, while regional climate marginalizes local weather over space and time. Tree species do not directly respond to climate, rather individuals respond to weather. Local microclimate data are important (Dobrowski, 2011), but yet unavailable for FIA plots. Rather than using an epidemiological approach to investigate individual tree health at fine scales (Clark *et al.*, 2011b; Clark *et al.*,

2012), we adopted an alternative approach, similar to Iverson and Prasad (1998), to aggregate FIA data from plots to ecoregions, a scale more compatible with regional climate.

At the ecoregion scale, we focused the analysis on nonzero observations, because we were interested in abundance pattern within a species' geographic range. On the one hand, we assumed our aggregated ecoregion data has only one source of zero observations: the species is located outside of its range so it cannot occur. In an average ecoregion, a zero observation implies zero seedling density or tree BA in all of the approximately 100 plots located in a geographic area over 7,000 km^2. On the other hand, focusing on nonzero observations greatly simplified the model and identified clear climate signals in species abundance data. Handling both zero and nonzero abundance using zero-inflated distributions is more challenging, as we found in a separate analysis (S. Ghosh, K. Zhu, A.E. Gelfand & J.S. Clark, unpublished data). Future studies on modeling zero-inflated data may be needed in this context.

2.4.3 Conclusions

The comparisons of juvenile vs. adult in both geographic space at local scale (Zhu *et al.*, 2012) and climate space at regional scale (this analysis) suggest that tree species are not yet migrating to track climate change, in agreement with modeling studies (Clark *et al.*, 2001) and increasing evidence from observational studies (Corlett & Westcott, 2013). Instead, here we show that the overall tendency is toward faster population turnover in warm and wet climates, consistent with physiological experiments (Saxe *et al.*, 2001), and observations across space (Stephenson & van Mantgem, 2005) and time (Phillips & Gentry, 1994; Phillips *et al.*, 2004). At biogeographic scales, eastern US forests are responding to climate change with faster turnover rates, and not yet with appreciable northward migration.

3 Prevalence and strength of density dependent tree recruitment in eastern US forests

3.1 Introduction

Density dependence (DD) has long been viewed as one of the important mechanisms maintaining species coexistence (MacArthur & Levins, 1967; Antonovics & Levin, 1980; Chesson, 2000; Clark, 2010; HilleRisLambers *et al.*, 2012), but studies continue to disagree on its role (Harms *et al.*, 2000; HilleRisLambers *et al.*, 2002; Comita *et al.*, 2010; Johnson *et al.*, 2012; Bagchi *et al.*, 2014). Diversity may be promoted when competition is concentrated within the species, a demographic penalty suffered by species that become locally abundant. At least part of the conflict could result from the fact that different studies evaluate the effects of different predictors, including adult distance or seedling density, on different responses, including recruitment densities, recruitment rates, or other demographic rates (Herrando-Perez *et al.*, 2012). Furthermore, it is difficult to generalize DD effects on diversity, because most DD studies are conducted on a single site. Among the few large-scale studies, results are contradictory (HilleRisLambers *et al.*, 2002; Johnson *et al.*, 2012). In this study, we investigate both the prevalence and strength of DD effects by introducing a more inclusive perspective that embraces the different predictor-response combinations. We argue that specific combinations can provide most insight and then evaluate using a forest inventory data set across the eastern United States.

We begin by clarifying how analyses of DD in the literature relate to one another. The three life stages that are typically involved in DD studies include seedlings, saplings, and trees, variously defined on the basis of size and/or age. These three stages can be represented by a system of equations,

$$\begin{cases} \dfrac{dx_1}{dt} = f(t) - m_1 x_1(t) - r x_1(t) \\ \dfrac{dx_2}{dt} = r x_1(t) - m_2 x_2(t) - g x_2(t) \\ \dfrac{dx_3}{dt} = g x_2(t) - m_3 x_3(t) \end{cases} \qquad 12$$

and a life cycle graph (Figure 3.1). Seedling abundance x_1 changes due to fecundity f, seedling mortality m_1, and growth from seedlings to saplings $r(t; \mathbf{z}(t))$, which depends on covariates $\mathbf{z}(t)$, including DD and other environmental variables. Recruitment $r(t; \mathbf{z}(t))$ is a per-capita rate, in most studies defined on a per-seedling basis. To simplify subsequent notation, we define recruitment density $R(t; \mathbf{z}(t)) = r(t; \mathbf{z}(t))x_1(t)$. We can also consider recruitment rate on a per-tree (adult) basis, $\lambda(t; \mathbf{z}(t)) = R(t; \mathbf{z}(t))/x_3(t)$. Sapling abundance x_2 changes due to recruitment r, sapling mortality m_2, and growth to the tree class g. Tree abundance x_3 changes due to growth g and tree mortality m_3.

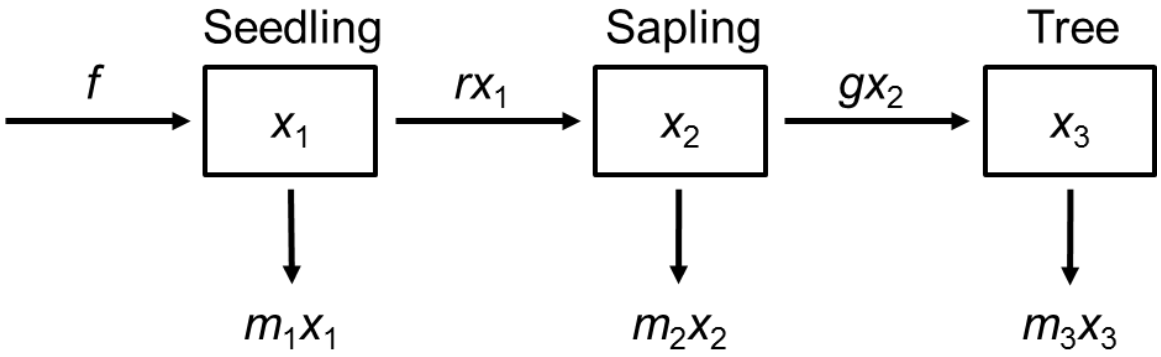

Figure 3.1: Simplified life cycle graph for a size-structured tree population. Seedlings (x_1), saplings (x_2), and trees (x_3) are classified by a continuum of diameter at breast height (DBH). Demographic transitions include fecundity (f), recruitment (r), growth (g), mortality for seedlings (m_1), saplings (m_2), and trees (m_3). Per-capita recruitment can be expressed as a per-seedling rate (r) or a per-tree (adult) rate ($\lambda = rx_1/x_3$).

Part of the disagreement in the literature is caused by the fact that the definition of "DD" can refer to different terms in this simple model. For example, to test the Janzen-Connell hypothesis (Connell, 1970; Janzen, 1970), most studies focus on seedling mortality (m_1) (Webb & Peart, 1999; HilleRisLambers *et al.*, 2002; Queenborough *et al.*, 2007; Comita & Hubbell, 2009; Bagchi *et al.*, 2010; Chen *et al.*, 2010; Comita *et al.*, 2010; Metz *et al.*, 2010; Kobe & Vriesendorp, 2011; Bai *et al.*, 2012; Lin *et al.*, 2012; Paine *et al.*, 2012; Lebrija-Trejos *et al.*, 2013; Piao *et al.*, 2013; Gripenberg *et al.*, 2014); while others quantify sapling and tree mortality (m_2 and m_3) (He & Duncan 2000; Hubbell *et al.* 2001; Peters 2003), growth rate (g) (Uriarte *et al.*, 2004; Newbery & Stoll, 2013), or seedling abundance (x_1) (Johnson *et al.*, 2012; Sheffer *et al.*, 2013). Direct tests of DD effects on recruitment (r, λ, or R) have all been conducted on a single site—Barro Colorado Island (BCI), yet even here there is disagreement: conclusions vary from limited DD effects on a few common species (Hubbell *et al.*, 1990; Condit *et al.*, 1992; Condit *et al.*, 1994), to strong DD effects on the majority of species (Wills *et al.*, 1997; Wills & Condit, 1999; Harms *et al.*, 2000). As the only exception outside of BCI, Bagchi *et al.* (2014) tested DD recruitment in Belize but found opposite relationship of DD strength and species abundance than previously reported from BCI (Comita *et al.*, 2010).

The stage assumed to predict DD likewise varies among studies, sometimes seedling density, other times adult density. The specific predictor-response combination reported in a given study is rarely justified as the one most promising for promoting diversity. In light of the range of conflicting results in the literature and the large number of predictor-response combinations that could be analyzed, it is worth asking which predictor and response variables are most likely to (i) promote diversity, and (ii) be identified in observational or experimental data?

In answer to the first question, the most efficacious DD (in terms of promoting diversity) occurs when there is a negative relationship between adult density and per-adult recruitment, $\frac{\partial \lambda}{\partial x_3} < 0$. Alternative relationships, such as large effects of seedling density on per-seedling recruitment $\frac{\partial r}{\partial x_1}$ or mortality $\frac{\partial m_1}{\partial x_1}$, need not translate to an important effect on population growth or to diversity. This also applies to the effects of adults on per-seedling recruitment $\frac{\partial r}{\partial x_3}$, on per-seedling mortality $\frac{\partial m_1}{\partial x_3}$, and on seedling density $\frac{\partial x_1}{\partial x_3}$. Compared with adults, seedlings can be heterogeneous and dynamic: seedlings undergo large changes in density that can have little or even no impact on population growth rate. In other words, the densities and demographics in seedling pools can be decoupled from long-term population growth rates. Since DD in seedling classes need not translate to canopy classes, and only adults contribute to the next generation, recruitment rates evaluated on the per-seedling basis are less relevant than the per-adult basis. The most efficacious DD results when recruitment is strong for species that are not abundant in the class responsible for seed production, the canopy.

The answer to the second question, which relationships might be most indicative of DD in data, also include the effects of adults on recruitment, expressed as a per-adult rate, $\frac{\partial \lambda}{\partial x_3}$. Here again, due to spatio-temporal variation in seedling densities, evidence of a DD signal in per-seedling rates can be difficult to demonstrate. We expect that effects of adults on recruitment to the sapling class, rather than the tree class, may provide more direct evidence of DD, due to the

long lag associated with recruitment to large size classes and to the fact that most postulated DD mechanisms (seed and seedling predation, pathogens, etc.) are expected to affect small seedlings.

Beyond the need to clarify the important stages for DD, there is also need to test effects across biogeographical scales and to include a large number of species. In this regard, forest inventory data provide unique opportunities to complement the understandings already gained from local sites (e.g., BCI). Recently, Johnson *et al.* (2012) found that for most tree species in eastern US forests, seedling abundance (x_1) is negatively correlated with conspecific tree abundance (x_3), a pattern that is consistent with negative DD. This relationship was strongest for rare species, which might be consistent with the interpretation that DD explains why some species are rare. However, a similar study by Sheffer *et al.* (2013) found a hump-shaped DD relationship between seedling abundance (x_1) and tree abundance (x_3) of *Quercus calliprinos* in Israel. In both cases the use of seedling abundance (x_1) as a surrogate for recruitment (r, λ, or R) could influence results. Seedlings can be abundant because fecundity (f) is high, seedling mortality (m_1) is low, or recruitment (r) is low. An abundance of seedlings does not require that fecundity is high and seedling mortality and recruitment are low. Therefore, tests on DD recruitment using seedling abundance are indirect.

In this study, we examine both the prevalence and strength of DD effects on per-capita recruitment and its relationship with tree species abundance in eastern US forests. We focus on DD effects on per-tree (adult) recruitment, but we also compare with per-seedling recruitment. Specifically, we ask the following questions on DD prevalence and strength.

1. Prevalence. Do the majority of species have DD effects in per-tree (λ) and per-seedling recruitment (r)? Are these DD effects mostly negative, especially in tree abundance on per-tree recruitment ($\frac{\partial \lambda}{\partial x_3} < 0$)?

2. Strength. Do conspecifics have stronger DD effects than heterospecifics? Does the strength of DD effects vary with overall species abundance (e.g., rare species advantage)?

To answer these questions, we make use of the data from the Forest Inventory and Analysis (FIA) program of the USDA Forest Service, with over one million stem observations for a continuum of size classes. For a range of tree species, we develop statistical models to examine the relationships between per-capita recruitment and neighboring densities through life history stages, controlling for climate variation at biogeographic scales. Our approach differs from previous studies in using seedling-to-sapling recruitment, rather than seedling abundance, to understand DD patterns in recruitment. To understand the prevalence of DD, we quantify the proportion of species with significant positive or negative effects. To understand the strength of DD, we determine the magnitude of effects among conspecifics and heterospecifics, and how it changes with overall species abundance.

3.2 Material and methods

3.2.1 Data

The USDA Forest Service's FIA program is the primary source for information about the extent, condition, status, and trends of forest resources in the United States (Smith *et al.*, 2009). FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships across the United States, resulting in national sample intensity of one plot per 2,428

ha (Bechtold & Patterson, 2005). Classified satellite imagery is used to identify forested land, which is defined as areas with at least 10% covered by tree species canopies, at least 0.4 ha in size, and at least 36.6 m wide. In forest land, FIA inventory plots consist of four, 7.2 m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Bechtold & Patterson, 2005). All trees (standing live and dead) with a diameter at breast height (DBH) of at least 12.7 cm are inventoried on forested subplots. Within each subplot, a 2.07 m radius microplot offset 3.66 m from subplot center is established where only live trees with a DBH between 2.5 and 12.7 cm are inventoried. Within each microplot, all live tree seedlings are tallied according to species. Conifer seedlings must be at least 15.2 cm in height with a root collar diameter less than 2.5 cm. Hardwood seedlings must be at least 30.5 cm in height with a root collar diameter less than 2.5 cm. Note that they are often well established stems, typically not first-year seedlings.

In this analysis, FIA data were extracted from 21,201 fully forested natural (non-plantation) plots with two censuses (during 1996 to 2011) in 31 eastern states from FIADB version 5.1 on May 5, 2012 (available online http://fia.fs.fed.us/). We restricted analysis to 50 common species with sufficient sample sizes (Table S1). We followed the FIA sampling design to divide the data into three size classes: (i) seedling (DBH < 2.54 cm), (ii) sapling (2.54 cm ≤ DBH < 12.7 cm), and (iii) tree (DBH ≥ 12.7 cm). For each species, we used seedling-to-sapling recruitment, rather than seedling abundance, as the basis for interpretation of recruitment. Individual stems were tracked for saplings and trees between the two censuses available from these sites, completed at an average interval of 5 yr. We defined total seedling-to-sapling recruitment as the number of new saplings that appeared for the first time in the 2nd census. Since FIA plots record each stem with species identity, we defined conspecific and heterospecific

neighboring density in three ways: (i) seedling density (ha^{-1}), (ii) sapling basal area ($m^2\ ha^{-1}$), and (iii) tree basal area ($m^2\ ha^{-1}$) in the 1st census.We focused on per-capita recruitment in two ways: (i) per-tree (adult) recruitment (λ, annual per conspecific tree basal area recruitment rate, $m^{-2}\ yr^{-1}$) and (ii) per-seedling recruitment (r, annual per conspecific seedling count recruitment rate, yr^{-1}), as defined in Equation 12. In other words, we used per-capita (tree or seedling) recruitment as the response and neighboring densities of seedlings, saplings, and trees as the predictors.

In addition, we controlled for effects of climate variation on DD at biogeographic scales. Climate data in this study were extracted from the 800 m resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) data set (available online http://prism.nacse.org/). Recognized as a high quality spatial climate data set in the United States, PRISM is an interpolation of meteorological station data to produce continuous, digital grid estimates of climatic parameters, with consideration of location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly *et al.*, 2008). We used long-term average climate data (1990 to 2010) corresponding to each FIA plot as the climate covariates. We extracted annual mean temperature (°C), ranging from 0 °C to 25 °C, and annual precipitation (mm), ranging from 550 mm to 1650 mm.

3.2.2 Analysis

We applied a zero-inflated Poisson (ZIP) distribution (Lambert, 1992) to model recruitment. For each species, we analyzed plots with either nonzero conspecific seedling or tree densities to focus on dynamics within the geographic range of the species (e.g., *Liriodendron tulipifera* in Figure 3.2). Recruitment must be zero when no seedling or tree occurs; DD is only relevant within geographic range as biologically meaningful (Johnson *et al.*, 2012). In these plots,

we used the zero-inflated model because recruitment can be absent for multiple reasons. Neighboring seedling, sapling, and tree densities were used as predictors to determine the strength of DD effects on recruitment. Climate variables helped account for the fact that relationships between recruitment and adult abundances could be influenced by climate effects on one or both of these variables.

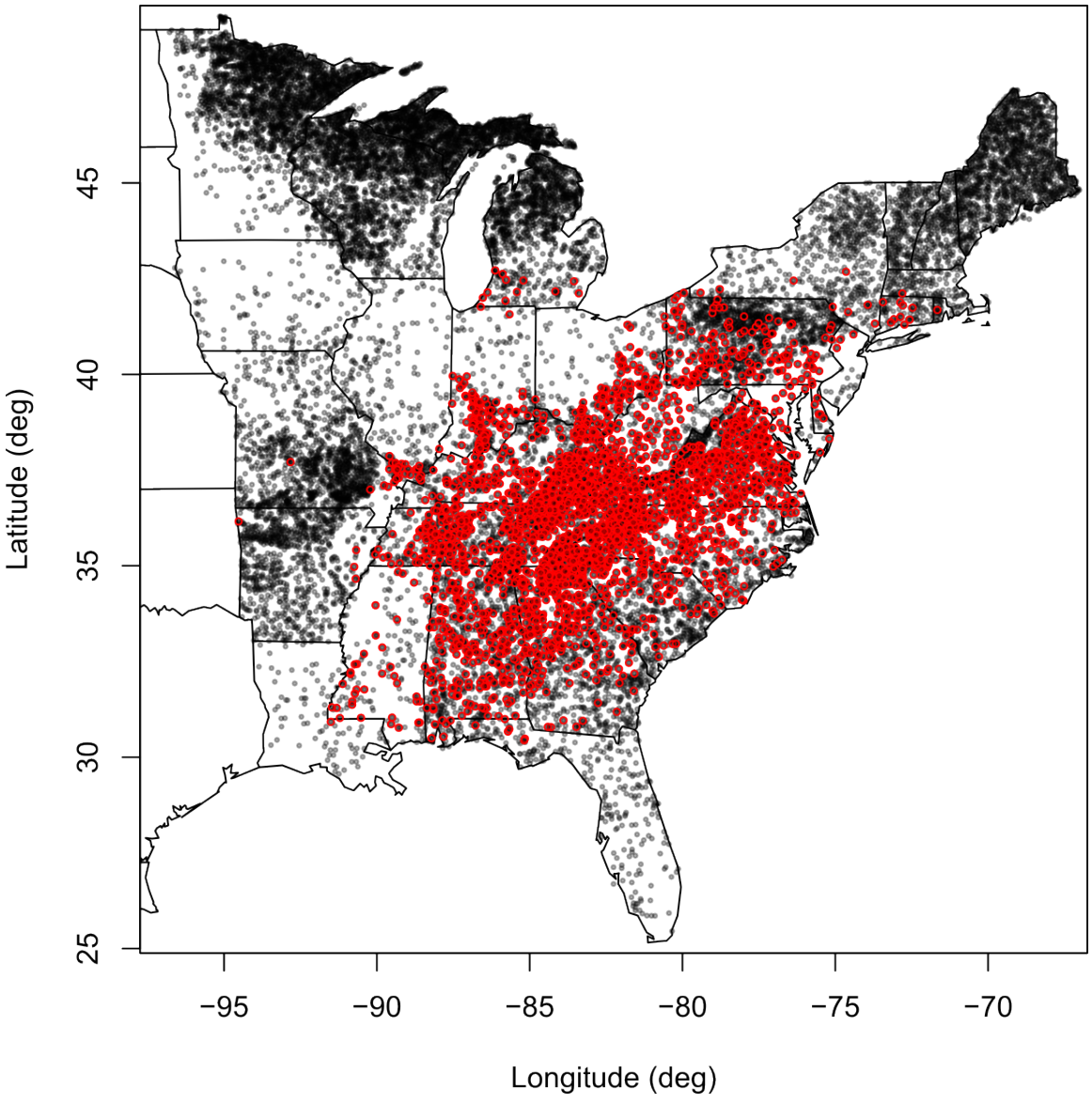

Figure 3.2: Forest Inventory and Analysis (FIA) plot locations (gray points) and occurrence of an example species *Liriodendron tulipifera* (red circles) in the eastern United States.

Recruitment was analyzed on the basis of repeated censuses of the same plot. The number of new saplings in plot i that appeared in the 2nd census y_i was modeled as a two-stage process: presence with probability θ_i, and abundance conditional on presence with a Poisson distribution,

$$y_i \sim \begin{cases} \text{Poisson}\left(A_i \Delta t_i \mu_i\right) & \text{with probability } \theta_i \\ 0 & \text{with probability } 1-\theta_i \end{cases} \quad (13)$$

where A_i is plot area (ha), Δt_i is the interval between censuses (yr). Per-capita recruitment is expressed in two ways: (i) $\mu_i = \lambda_i x_{3,i}$, per-tree recruitment λ_i (m^{-2} yr^{-1}) where $x_{3,i}$ is the conspecific tree basal area (m^2 ha^{-1}); and (ii) $\mu_i = r_i x_{1,i}$, per-seedling recruitment r_i (yr^{-1}) where $x_{1,i}$ is the conspecific seedling density (ha^{-1}). Models for per-capita recruitment and presence are

$$\begin{aligned} \log \lambda_i &= X_i \beta^{(\lambda)} \text{ or } \log r_i = X_i \beta^{(r)} \\ \text{logit}\, \theta_i &= Z_i \gamma \end{aligned} \quad (14)$$

The covariates in X_i are six neighboring densities, i.e., conspecific and heterospecific seedling density (x_1, ha^{-1}), sapling basal area (x_2, m^2 ha^{-1}), and tree basal area (x_3, m^2 ha^{-1}). Due to the nonlinearity of the model, coefficients $\beta^{(\lambda)}$ and $\beta^{(r)}$ are not direct interpretable. Instead, we interpreted the DD effects as the sensitivity of per-capita recruitment to neighboring density,

$$\frac{\partial \lambda}{\partial x_j} = \frac{\partial \exp\left(X\beta^{(\lambda)}\right)}{\partial x_j} = \beta_j^{(\lambda)} \exp\left(X\beta^{(\lambda)}\right)$$
$$\frac{\partial r}{\partial x_j} = \frac{\partial \exp\left(X\beta^{(r)}\right)}{\partial x_j} = \beta_j^{(r)} \exp\left(X\beta^{(r)}\right) \quad (15)$$

where x_j is the jth neighboring covariate (seedling, sapling, or tree density). These sensitivities quantify how much per-capita recruitment change with respect to change in each neighboring density. We evaluated these sensitivities at the same level by setting X to the median densities for all species. Finally, the covariates in Z_i include climate variables: temperature (T_i, °C), precipitation (P_i , mm), and quadratic and interaction terms ($T_i^2, P_i^2, T_i \cdot P_i$). Climate covariates were limited to the presence portion of the model because inclusion in both results in overfitting (Zhu *et al.*, 2014).

Model selection was implemented to determine variables that explain recruitment. First, we used logistic regression to choose climate inputs based on the best-fitting model for recruitment presence (0 or 1). For each species we chose the best four out of 32 models (2^5 combinations of main effects and interactions for five climate covariates) based on the Akaike information criterion (AIC). We subsequently fitted these four models using the full ZIP model in the Bayesian framework, and chose the best model based on the deviance information criterion (DIC). In this way only significant DD effects were included in the final model.

All covariates (X_i, Z_i) were centered and scaled to unit standard deviation to fit the model, but they were recovered to the original scale to interpret DD effects as sensitivities (Equation 15). For the Bayesian model, non-informative priors $\beta, \gamma \sim N\left(0, 10^2\right)$ were used. Posterior distributions were simulated using Markov chain Monte Carlo (MCMC). Convergence was

checked by both visually assessing trace plots and Geweke diagnostics after 10,000 iterations for each species. All analyses were performed in R version 3.0.0 (R Development Core Team, 2013).

3.3 Results

Per-tree (adult) recruitment rate (λ) had significant DD effects for a large number of species (Table C1). In Figure 3.3, species are included for which covariates were chosen by model selection. Among the 50 species, DD effects were significant for 43 species (86% of all species) from conspecific seedlings; 31 species (62%) from heterospecific seedlings; 38 species (76%) from conspecific saplings; 30 species (60%) from heterospecific saplings; 50 species (100%) from conspecific trees; and 40 species (80%) from heterospecific trees (Figure 3.3). In other words, the majority of these species were identified to have significant DD effects on per-tree recruitment.

Across species, these significant DD effects on per-tree recruitment were mostly negative. Figure 3.3 shows DD effects from all neighboring covariates (sensitivity $\frac{\partial \lambda}{\partial x_j}$ in Equation 15), where a negative coefficient indicates the annual per conspecific tree basal area recruitment rate (λ) is reduced by increasing neighboring seedling, sapling, or tree density—a negative DD effect. Per-tree recruitment was positively associated with densities of conspecific seedlings for all species (100%, Figure 3.3a) but negatively associated with heterospecific seedlings for most species (87%, Figure 3.3b). For most species per-tree recruitment was positively associated with both conspecific saplings (92%, Figure 3.3c) and heterospecific saplings (63%, Figure 3.3d). Negative DD effects on per-tree recruitment from conspecific trees were ubiquitous (100%, Figure 3.3e) and nearly as pervasive from heterospecific trees (92%, Figure 3.3f).

Across all species, DD effects on per-tree recruitment from conspecifics were stronger than heterospecifics. The average sensitivities ($\frac{\partial \lambda}{\partial x_j}$ in Equation 15, Figure 3.3) were higher from the conspecific than heterospecific neighbors. In other words, the change in the annual conspecific per-tree basal area recruitment rate (λ) was greater for the same amount of change in conspecific than heterospecific neighboring densities (x_j's). Averaged across all species, per-tree recruitment increased 19 m^{-2} yr^{-1} for each additional conspecific seedling density (ha^{-1}, Figure 3.3a) but decreased 5 m^{-2} yr^{-1} for each additional heterospecific seedling density (ha^{-1}, Figure 3.3b). Average per-tree recruitment increased 1.3 m^{-2} yr^{-1} for each additional conspecific sapling basal area (m^2 ha^{-1}, Figure 3.3c) and 0.3 m^{-2} yr^{-1} for each additional heterospecific sapling basal area (m^2 ha^{-1}, Figure 3.3d). In contrast, average per-tree recruitment decreased 3.4 m^{-2} yr^{-1} for each additional conspecific tree basal area (m^2 ha^{-1}, Figure 3.3e) and 0.3 m^{-2} yr^{-1} for each additional heterospecific tree basal area (m^2 ha^{-1}, Figure 3.3f).

The strength of DD effects on per-tree recruitment did not vary with species abundance. In Figure 3.3, we ranked DD effects by species abundance, defined as the average sapling and tree basal areas (m^2 ha^{-1}) in all 21,201 plots. It spanned more than four orders of magnitude, from common species (e.g., *Pinus taeda* 1.503 m^2 ha^{-1}, *Quercus alba* 0.973 m^2 ha^{-1}) to rare species (e.g., *Cercis canadensis* 0.005 m^2 ha^{-1}, *Persea borbonia* 0.010 m^2 ha^{-1}). However, we found no systematic relationship (increasing or decreasing) between DD effects and species abundance.

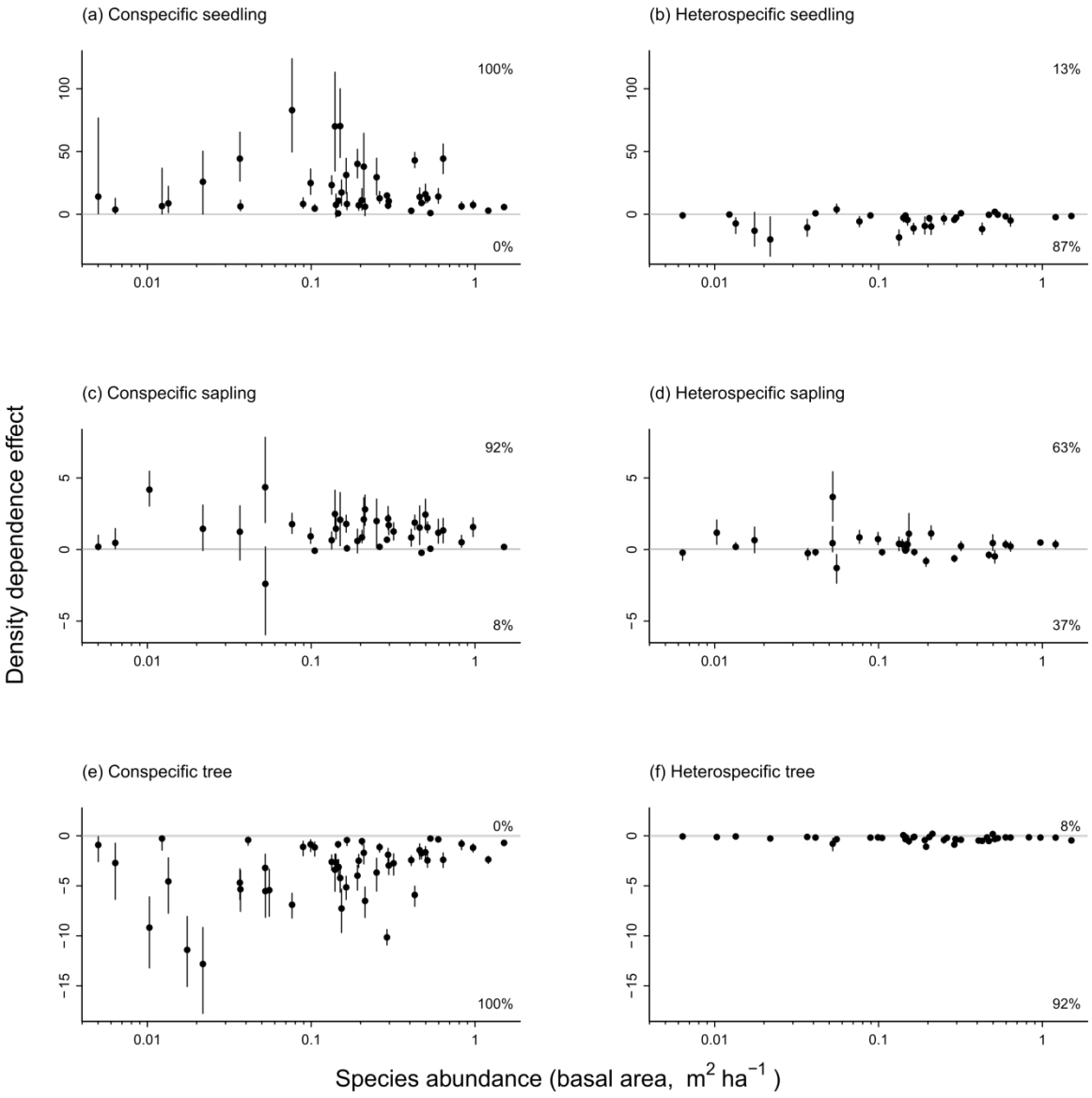

Figure 3.3: Density dependence (DD) effects, defined as per-tree (adult) recruitment (λ) sensitivity to neighboring densities, plotted by species abundance. Each species is summarized by a posterior mean (point) and 95% credible interval (vertical line) for variables included in the selected model. Negative coefficients indicate species for which per-capita recruitment is reduced by neighboring densities. Numbers of species for which DD is positive and negative are summarized by percentages at the corners of each panel.

Per-seedling recruitment rate (r) also had significant DD effects for a large number of species (Figure 3.4; Table C2). Among the 50 species, DD effects were significant for 48 species

(96%) from conspecific seedlings; 30 species (60%) from heterospecific seedlings; 36 species (72%) from conspecific saplings; 24 species (48%) from heterospecific saplings; 26 species (52%) from conspecific trees; and 42 species (84%) from heterospecific trees (Figure 3.4).

Across species, these significant DD effects on per-seedling recruitment were also mostly negative. DD effects from conspecific and heterospecific seedlings were overwhelmingly negative (100% and 93%, Figure 3.4a and b). By contrast, per-seedling recruitment was positively associated with conspecific saplings (83%, Figure 3.4c) and, to a lesser degree, heterospecific saplings (54%, Figure 3.4d). Finally, negative DD effects of trees were pervasive both for conspecifics (73%, Figure 3.4e) and heterospecifics (93%, Figure 3.4f).

Similar to per-tree recruitment, per-seedling recruitment generally had stronger DD effects from conspecifics than heterospecifics. The average sensitivities ($\frac{\partial r}{\partial x_j}$ in Equation 15, Figure 3.4) suggest that the change in the annual per conspecific seedling count recruitment rate (r) was greater for the same amount of change in conspecific than heterospecific neighboring densities (x_j's). Averaged across all species, per-seedling recruitment decreased 0.1 yr^{-1} for each additional conspecific seedling density (ha^{-1}, Figure 3.4a) and 0.02 yr^{-1} for each additional heterospecific seedling density (ha^{-1}, Figure 3.4b). In contrast, average per-seedling recruitment decreased 0.004 yr^{-1} for each additional conspecific sapling basal area (m^2 ha^{-1}, Figure 3.4c) and 0.0008 yr^{-1} for each additional heterospecific sapling basal area (m^2 ha^{-1}, Figure 3.4d). Average per-seedling recruitment increased 0.0006 yr^{-1} for each additional conspecific tree basal area (m^2 ha^{-1}, Figure 3.4e) but decreased 0.0006 yr^{-1} for each additional heterospecific tree basal area (m^2 ha^{-1}, Figure 3.4f).

Similar to per-tree recruitment, the strength of DD effects on per-seedling recruitment did not vary with species abundance.

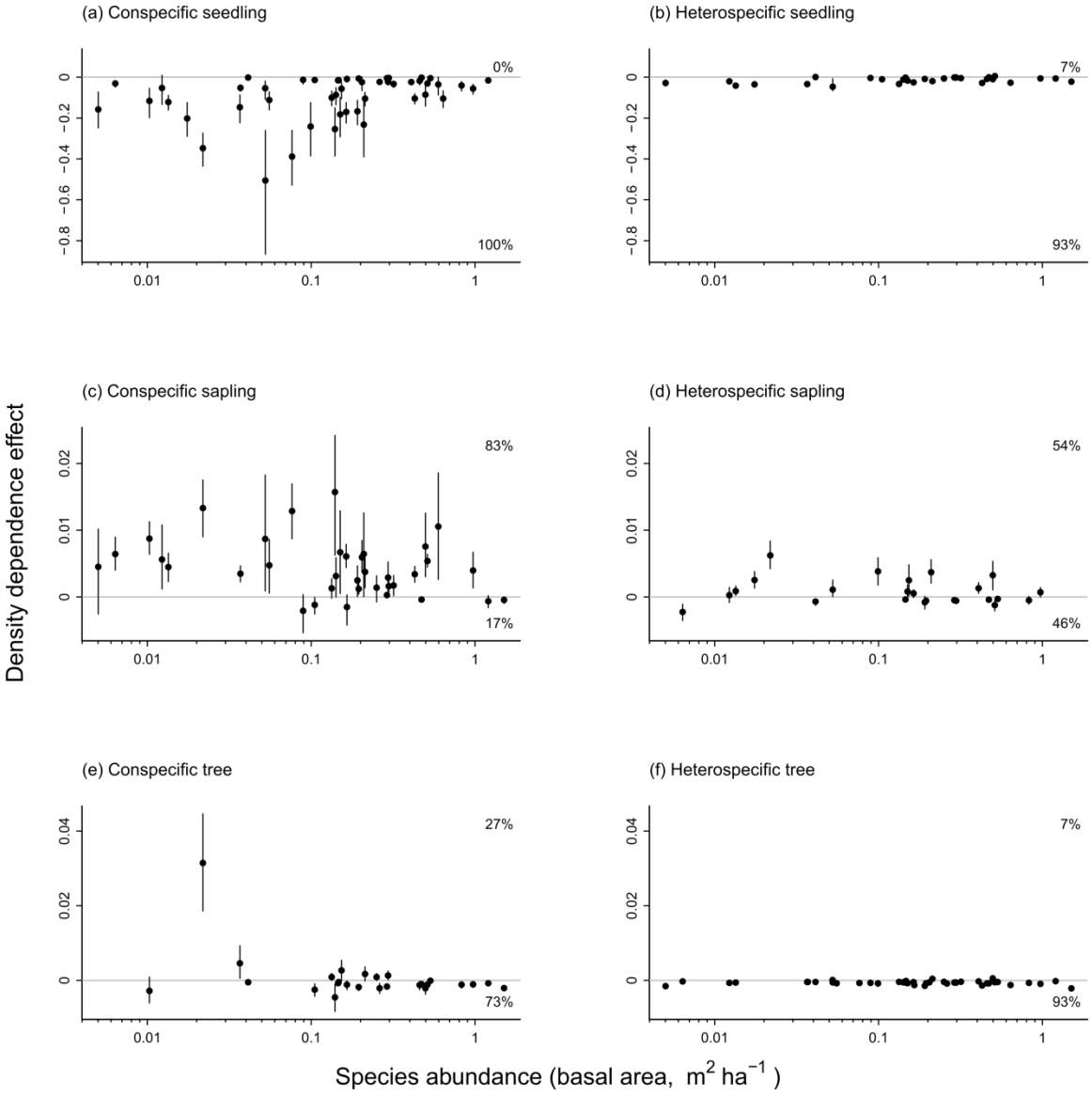

Figure 3.4: DD effects, defined as per-seedling recruitment (*r*) sensitivity to neighboring densities, plotted by species abundance. Symbolism follows Figure 3.3.

Evaluating DD effects on per-tree and per-seedling recruitment at other levels of neighboring densities (*X* in Equation 15) led to qualitatively similar results. Climate effects were

much less significant than DD effects, with balanced negative and positive coefficients. We included all coefficients in Tables C1 and C2.

3.4 Discussion

Our results show that DD effects on recruitment are pervasive, mostly negative, and stronger for conspecifics than heterospecifics, but they do not vary systematically with overall species abundance. DD effects pervasively regulate population dynamics, as suggested by the negative relationship in the most indicative predictor-response combination, i.e., between adult density and per-adult recruitment ($\frac{\partial \lambda}{\partial x_3} < 0$,Figure 3.3e). The fact that most conspecifics have stronger DD effects than heterospecifics is consistent with the host-specific predictions of the Janzen-Connell hypothesis. By focusing on per-adult recruitment, we provide the most direct evidence of DD effects that regulate population dynamics for a suite of species in eastern US forests.

The prevalence of DD effects on recruitment is demonstrated by both per-tree and per-seedling rates through multiple life history stages (seedling, sapling, and tree). Different DD effects through life stages are likely to be explained by different mechanisms at local scales. For per-tree recruitment, the positive DD effects from conspecific seedlings could be caused by fecundity—more seedlings in, more saplings out (Figure 3.3a). The negative DD effects from heterospecific seedlings could be caused by competition from crowding of seedling neighbors (Figure 3.3b). The positive DD effects from both conspecific and heterospecific saplings could be a consequence of high recruitment into the sapling pool that translate to high sapling abundance, rather than the cause of abundant saplings (Figure 3.3c and d). The negative DD effects from both conspecific and heterospecific trees might be due to canopy shading that inhibit understory

recruitment by reducing light, moisture, etc. Within each species, it implies that more adults lead to fewer per-capita recruits, an important feature of population regulation. For per-seedling recruitment, the DD effects are similar to per-tree recruitment, except from conspecific seedlings (Figure 3.4a).

The strength of DD effects is greater from conspecifics than heterospecifics for all life history stages, but it does not differ among common and rare species. Differences between conspecifics and heterospecifics support the Janzen-Connell hypothesis as an important regulating mechanism at local scales. However, lack of relationships with species abundance does not inspire confidence that DD could promote diversity across biogeographical gradients. Local observations suggest that a tree canopy could exert strong control on the understory dynamics, but the effects drop off quickly with distance and are typically not significant beyond 30 m (Hubbell *et al.*, 2001). Janzen-Connell hypothesis is likewise a local mechanism, since the actions of host-restricted agents (e.g., microarthropods, fungi, pathogens) operate 50 m at most (Terborgh, 2012).

Our results are consistent with other findings that DD effects on recruitment are pervasive. Using 50-ha plot tree census data in BCI, Wills *et al.* (1997) found per-tree recruitment has significant negative DD effects from conspecific trees for the majority of the 84 most common species. Likewise, Wills and Condit (1999) found pervasive negative correlation between recruitment and conspecific tree density in two 50-ha rainforest plots, one in BCI and the other in Pasoh, Malaysia. These are consistent with our findings that conspecific trees have strong negative DD effects on per-tree recruitment for all species (100%, Figure 3.3e). Per-seedling recruitment likewise has pervasive DD effects from conspecific seedlings in tropical forests in BCI (Harms *et al.*, 2000) and Belize (Bagchi *et al.*, 2014). These are consistent with our findings

that conspecific seedlings have strong negative DD effects on per-seedling recruitment for all species (100%, Figure 3.4a). Note that per-seedling recruitment is less relevant at population level than per-tree recruitment, because seedling pools are heterogeneous and dynamic. We therefore propose focusing on per-tree, rather than per-seedling, recruitment rate. Regardless, all these results demonstrate that DD recruitment is a pervasive effect in single sites and across biogeographic extent.

Our further comparisons support the findings that conspecifics have stronger DD effects than heterospecifics, but do not support that DD effects vary with species abundance. Many studies focus on seedling survival and generally agree that survival decreases with increasing neighboring densities. For example, HilleRisLambers *et al.* (2002) found strong DD effects in seedling survival, but its prevalence does not vary with latitudinal gradient, suggesting that DD effects are equally important in many forests. Using seedling and tree census data in BCI, Comita *et al.* (2010) found seedling survival has stronger DD effects from conspecific than heterospecific neighbors, and rare species suffer stronger negative DD effects than common species. These results on seedling survival are in line with our findings in per-seedling recruitment, where conspecifics have stronger effects than heterospecifics (Figure 3.4a, b, e, f). Across geographic gradient in eastern US forests, Johnson *et al.* (2012) found stronger negative DD effects from conspecific than heterospecific seedling and tree abundances. In addition, they found this relationship to be stronger among rare than common species. Instead of seedling abundance, we directly focused on seedling-to-sapling recruitment, and we also found negative DD effects on per-seedling recruitment are stronger from conspecifics than heterospecifics (Figure 3.4). However, our comparisons do not show the difference in DD effects along species abundance gradient.

Our analysis comes with several important caveats. The DD patterns we found might be influenced by the fact that nearly all eastern US forests are in some stage of succession. The success of seedlings or saplings with respect to adults varies with succession in a systematic way. A species invading a stand has few adults and high recruitment; whereas a species losing ground to others later in succession has many adults and low recruitment. Another factor that apparently varies in the data set is canopy openness. Openness supports high seedling densities – much higher than can recruit to saplings, hence strong negative DD. To the contrary, deep shade under a mature canopy will greatly reduce seedling or sapling densities with perhaps mixed consequences for DD. We examined our patterns for species by shade-tolerance classes and did not find a tendency among species groups. In addition, due to lack of locally informed covariates, plot-scale models such as this analysis are always challenging to fit (Zhu *et al.*, 2014). Our model aims to understand DD effects on recruitment, and it has limited capacity in predictions without informative variables at local scales. Because FIA plots are small (0.067 ha), we were unable to conduct a spatial analysis on the neighborhood. More detailed understanding of how crowding and shading effects lead to DD pattern requires analyses explicitly including spatial arrangement of stems.

Despite caveats that must apply to analyses of forest inventory data, we found pervasive DD effects, stronger from conspecifics than heterospecifics, on per-capita tree recruitment rate. By explicitly focusing on per-adult recruitment, our results provide the most direct evidence that DD effects are regulating population dynamics. Our direct comparisons between conspecific and heterospecific neighbors are consistent with the Janzen-Connell hypothesis which emphasizes host-specific regulation as an important mechanism to maintain species diversity. Across eastern

US forests, tree populations are regulated by pervasive DD effect on recruitment, with stronger controls from conspecific than heterospecific neighbors.

Appendix A: Supporting information for Chapter 1

Table A1: Mean latitudinal range expansion (positive) or contraction (negative) at the northern and southern boundaries for the seedling vs. tree and sapling vs. large tree comparisons (Equation 1). Gray cells indicate mean ± standard error does not include zero.

Species	Seedling vs. tree		Sapling vs. large tree	
	N boundary	S boundary	N boundary	S boundary
Acer barbatum	–0.219	–0.420	–0.203	0.029
Acer nigrum	–0.298	–0.639	–0.745	–0.448
Aesculus flava	0.015	0.955	–0.310	0.259
Aesculus glabra	0.668	0.928	–0.147	0.144
Alnus glutinosa	0.236	–0.406	0.000	0.000
Asimina triloba	–0.262	2.014	0.998	1.897
Betula lenta	–0.049	–0.074	0.089	–0.077
Betula nigra	–1.792	–1.059	–1.918	–0.675
Carya alba	–0.376	–0.055	–0.512	0.031
Carya aquatica	0.115	–0.638	–0.117	–0.640
Carya cordiformis	–0.439	–0.565	–0.204	–0.316
Castanea dentata	–0.759	0.293	–0.042	0.769
Carya glabra	–0.332	–0.182	–0.662	0.147
Carya illinoinensis	–1.169	–0.901	–0.719	–0.960
Carya laciniosa	–0.338	–1.542	–0.677	–1.529
Carya ovata	–0.251	–0.302	0.070	–0.341
Catalpa speciosa	–6.414	6.074	0.000	0.000
Carya texana	0.078	–0.102	–0.027	–0.691
Cercis canadensis	–0.481	–0.167	–0.034	0.973
Celtis laevigata	0.072	–0.914	–0.208	–0.720
Celtis occidentalis	–0.875	–0.567	–0.887	–0.564
Chamaecyparis thyoides	1.503	–0.605	–0.199	–0.084
Cornus florida	0.088	–0.542	0.489	–0.244
Diospyros virginiana	–1.082	0.165	–0.611	0.124
Fraxinus quadrangulata	0.277	–0.670	0.463	0.311
Gleditsia aquatica	–0.475	–1.723	–1.172	–0.610
Gleditsia triacanthos	–1.667	–0.386	–1.024	–1.192
Gordonia lasianthus	0.222	0.249	0.141	–0.145
Gymnocladus dioicus	–0.789	–0.645	–3.340	2.111
Ilex opaca	0.410	–0.060	0.399	–0.032
Juglans cinerea	–1.962	–2.989	–0.126	–1.425

Juglans nigra	–0.164	–0.514	–0.172	–0.904
Juniperus virginiana	–0.981	–0.286	–0.372	–0.493
Liquidambar styraciflua	–0.128	–0.218	–0.564	–0.091
Liriodendron tulipifera	–0.278	–0.275	–0.573	–0.107
Magnolia acuminata	–0.166	0.059	–0.010	–0.035
Magnolia grandiflora	–0.256	–0.508	0.001	–0.170
Magnolia macrophylla	–0.144	–0.161	–0.008	–0.554
Maclura pomifera	–1.280	0.339	–0.529	–0.190
Magnolia virginiana	–0.111	–0.285	–0.030	–0.250
Morus rubra	–0.756	–0.998	–0.603	0.009
Nyssa aquatica	0.004	–0.809	–0.530	–0.470
Nyssa biflora	–0.341	–0.257	–0.348	–0.144
Nyssa ogeche	1.325	–0.248	–0.303	–0.055
Nyssa sylvatica	–0.190	–0.342	–0.430	–0.003
Oxydendrum arboreum	–0.128	–0.220	–0.107	–0.030
Persea borbonia	–0.114	0.011	0.240	–0.044
Pinus clausa	–0.370	–0.073	–0.059	–0.037
Pinus echinata	–0.183	–0.784	–0.544	–0.415
Pinus elliottii	–0.290	–0.198	–0.326	–0.047
Pinus glabra	–0.083	–0.138	–0.326	–0.067
Pinus palustris	–0.001	–0.367	–0.267	–0.272
Pinus pungens	–0.594	–0.370	–0.093	–0.250
Pinus rigida	–0.836	–0.537	–0.295	–0.451
Pinus serotina	–0.344	–0.501	–0.577	–0.189
Pinus taeda	–0.206	–0.069	–0.091	–0.130
Pinus virginiana	–0.580	–0.075	–0.409	–0.051
Platanus occidentalis	–0.959	–0.620	–0.208	–0.299
Prunus americana	–0.500	0.081	0.363	4.387
Quercus alba	–0.583	–0.031	–0.615	0.046
Quercus bicolor	–1.308	–2.088	–1.276	–1.853
Quercus coccinea	–0.058	–0.004	–0.225	0.058
Quercus ellipsoidalis	0.112	–1.125	–0.138	–0.961
Quercus falcata	–0.375	–0.118	–0.845	–0.039
Quercus ilicifolia	0.324	0.194	0.948	–0.360
Quercus imbricaria	–0.339	–0.118	–0.482	–0.414
Quercus laevis	–0.011	–0.155	–0.228	–0.123
Quercus laurifolia	0.276	–0.154	–0.081	–0.416
Quercus lyrata	–0.713	–0.455	–0.989	–0.082

Quercus marilandica	–0.639	0.071	–0.809	–0.031
Quercus margarettiae	–0.003	0.384	0.057	0.170
Quercus michauxii	0.318	–0.808	–1.179	–0.361
Quercus muehlenbergii	–0.630	1.078	–0.404	–0.040
Quercus nigra	–0.045	–0.156	–0.159	–0.074
Quercus palustris	0.092	–1.103	–0.949	–1.714
Quercus phellos	0.010	–0.207	–0.595	–0.100
Quercus prinus	0.185	–0.017	–0.010	0.159
Quercus shumardii	–0.474	–0.995	–1.457	–0.468
Quercus sinuata var. *sinuata*	–0.241	–0.199	0.190	–0.181
Quercus stellata	–0.241	–0.060	–0.821	–0.009
Quercus texana	–0.847	0.042	–0.640	–0.708
Quercus velutina	–0.536	0.057	–0.275	0.187
Robinia pseudoacacia	–0.439	–0.173	0.700	–0.645
Sassafras albidum	–0.364	0.345	–0.079	1.098
Salix nigra	–1.497	–0.539	–0.171	–0.624
Sideroxylon lanuginosum	1.883	–1.562	–0.445	2.291
Taxodium distichum	–0.289	–0.113	–0.990	–0.240
Tilia americana var. *heterophylla*	0.750	–1.580	–0.284	–0.867
Ulmus alata	0.075	–0.142	–0.037	–0.235
Ulmus crassifolia	–1.001	–0.535	–0.796	–0.030
Ulmus rubra	–1.464	–0.669	–0.843	–0.566
Ulmus thomasii	–1.360	0.660	0.277	–0.599

Table A2: Correlation between species range shift and 20th century temperature change at the northern and southern boundaries for the seedling vs. tree and sapling vs. large tree comparisons (ρ_T in Equation 2). Positive correlation at northern boundary implies range expands as temperature increases; while negative correlation at southern boundary implies range contracts as temperature increases. Species with fewer than three observations are not included (shown as "—").

Species	Seedling vs. tree		Sapling vs. large tree	
	N boundary	S boundary	N boundary	S boundary
Acer barbatum	0.422	0.355	0.371	–0.134
Acer nigrum	–0.074	–0.081	–0.314	0.283
Aesculus flava	–0.113	–0.348	0.608	–0.183
Aesculus glabra	–0.687	–0.604	0.158	–0.340
Alnus glutinosa	0.719	–0.777	—	—
Asimina triloba	–0.103	–0.162	–0.550	0.681
Betula lenta	–0.168	–0.049	–0.102	0.379
Betula nigra	0.283	0.347	0.500	0.224
Carya alba	0.134	0.057	0.420	–0.430
Carya aquatica	0.163	0.437	–0.144	0.167
Carya cordiformis	0.465	0.354	0.220	–0.034
Castanea dentata	0.417	–0.108	–0.011	–0.356
Carya glabra	0.176	–0.292	0.262	–0.532
Carya illinoinensis	0.235	–0.449	0.294	0.110
Carya laciniosa	0.276	–0.305	–0.030	–0.149
Carya ovata	0.204	–0.218	–0.130	–0.066
Catalpa speciosa	—	—	—	—
Carya texana	0.158	0.133	–0.217	0.196
Cercis canadensis	–0.496	0.603	–0.167	0.166
Celtis laevigata	0.463	–0.225	0.181	0.038
Celtis occidentalis	0.185	0.268	0.364	0.062
Chamaecyparis thyoides	–0.124	0.048	–0.310	–0.349
Cornus florida	–0.200	0.132	0.079	0.136
Diospyros virginiana	0.145	0.255	0.285	–0.518
Fraxinus quadrangulata	–0.118	0.565	–0.312	–0.527
Gleditsia aquatica	–0.531	–0.399	0.315	0.200
Gleditsia triacanthos	0.368	0.014	–0.061	–0.040
Gordonia lasianthus	0.064	0.115	–0.296	0.256
Gymnocladus dioicus	0.645	–0.261	0.884	–0.886
Ilex opaca	–0.397	0.134	–0.226	–0.007

Juglans cinerea	0.339	–0.104	–0.383	0.053
Juglans nigra	–0.332	–0.046	0.186	0.009
Juniperus virginiana	0.087	0.143	0.077	0.223
Liquidambar styraciflua	0.007	–0.007	0.425	–0.168
Liriodendron tulipifera	0.242	0.099	0.506	–0.228
Magnolia acuminata	–0.244	0.302	–0.228	–0.330
Magnolia grandiflora	–0.173	–0.019	0.452	–0.384
Magnolia macrophylla	0.240	–0.085	–0.008	–0.169
Maclura pomifera	0.480	–0.496	0.317	–0.327
Magnolia virginiana	0.067	–0.182	0.069	–0.002
Morus rubra	–0.643	–0.159	0.310	–0.320
Nyssa aquatica	0.135	0.072	0.413	0.279
Nyssa biflora	0.631	–0.023	0.551	–0.061
Nyssa ogeche	–0.257	–0.747	–0.994	0.933
Nyssa sylvatica	–0.102	0.277	0.425	0.010
Oxydendrum arboreum	0.092	0.158	0.416	0.116
Persea borbonia	0.108	0.114	0.018	–0.546
Pinus clausa	–0.054	–0.750	–0.202	–0.779
Pinus echinata	–0.056	0.108	0.093	0.017
Pinus elliottii	0.232	–0.254	–0.218	–0.584
Pinus glabra	0.048	–0.309	0.113	–0.015
Pinus palustris	–0.205	0.593	0.235	–0.229
Pinus pungens	—	—	0.723	0.352
Pinus rigida	0.089	–0.328	0.201	–0.507
Pinus serotina	–0.020	0.777	0.081	–0.637
Pinus taeda	–0.056	0.281	0.312	–0.182
Pinus virginiana	0.311	–0.143	0.088	0.262
Platanus occidentalis	0.339	–0.174	0.223	–0.078
Prunus americana	–0.246	0.505	–0.798	0.984
Quercus alba	0.475	–0.037	0.284	–0.305
Quercus bicolor	0.372	–0.082	0.524	–0.147
Quercus coccinea	–0.334	–0.078	0.461	0.048
Quercus ellipsoidalis	–0.207	0.412	–0.271	0.446
Quercus falcata	0.417	–0.481	0.464	–0.339
Quercus ilicifolia	0.015	0.127	0.253	0.412
Quercus imbricaria	–0.286	–0.241	–0.042	0.162
Quercus laevis	0.434	0.253	–0.001	0.029
Quercus laurifolia	–0.043	–0.450	0.205	–0.101

Quercus lyrata	0.065	0.001	–0.314	0.059
Quercus marilandica	0.233	–0.164	0.071	–0.330
Quercus margarettiae	0.619	0.221	–0.189	0.452
Quercus michauxii	0.359	–0.205	0.063	0.136
Quercus muehlenbergii	–0.126	0.535	0.112	–0.221
Quercus nigra	0.006	–0.584	0.085	–0.437
Quercus palustris	–0.111	–0.240	–0.094	0.312
Quercus phellos	0.194	–0.485	0.312	–0.476
Quercus prinus	–0.417	–0.436	–0.410	–0.308
Quercus shumardii	–0.142	–0.039	0.555	0.120
Quercus sinuata var. *sinuata*	–0.482	–0.566	0.948	0.704
Quercus stellata	0.232	–0.379	0.243	–0.249
Quercus texana	0.313	0.575	0.581	0.161
Quercus velutina	0.425	–0.114	0.120	–0.374
Robinia pseudoacacia	0.318	–0.579	0.185	0.333
Sassafras albidum	0.174	–0.154	–0.243	–0.220
Salix nigra	0.277	0.166	–0.032	–0.072
Sideroxylon lanuginosum	–0.928	–0.144	–0.281	–0.531
Taxodium distichum	0.133	0.215	0.210	0.232
Tilia americana var. *heterophylla*	0.333	0.598	–0.249	0.188
Ulmus alata	–0.317	0.150	–0.260	–0.049
Ulmus crassifolia	0.303	0.211	–0.388	0.685
Ulmus rubra	0.065	0.159	–0.302	–0.287
Ulmus thomasii	0.496	–0.349	0.493	–0.435

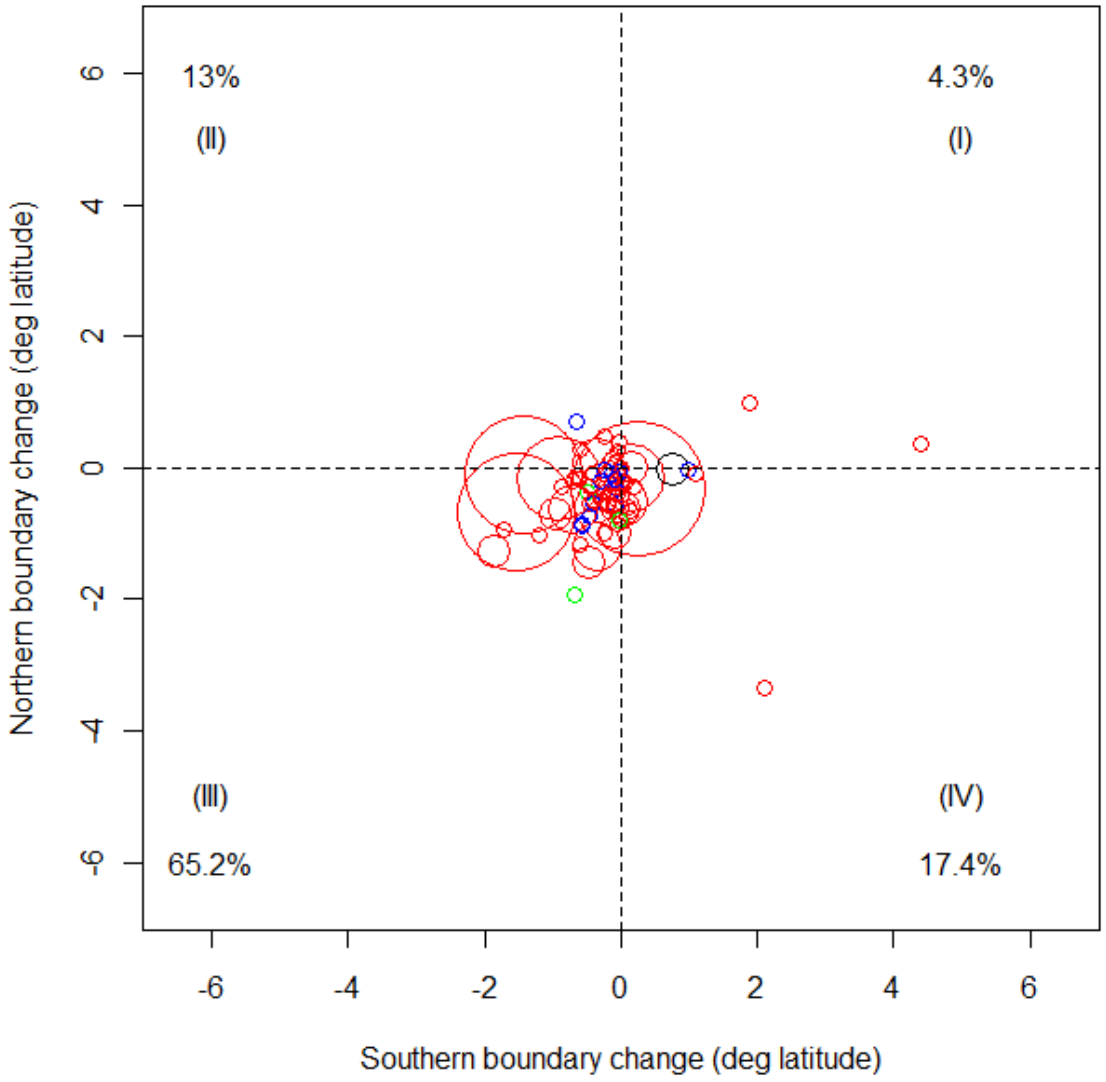

Figure A1: Latitudinal range change at southern (5th percentile) and northern (95th percentile) boundaries from the sapling vs. large tree comparison. Same notation as Figure 1.5.

Appendix B: Supporting information for Chapter 2

Table B1: Model fit measures and optimal climate conditions for all 65 species. Model fit is summarized by the goodness-of-fit (Equation 6), ranging from 0 to 1, for seedlings (R_Y^2) and trees (R_Z^2) at ecoregion and plot scales. For each species, the ecoregion-level model performs better than the plot-level model. Optimal climate is calculated as the annual mean temperature ($\tilde{T}$) and annual precipitation ($\tilde{P}$) weighted by the predicted seedling and tree abundances (Equations 7 and 8). For the majority of species, the turnover hypothesis is supported as the seedling surface has higher optimal temperature and/or precipitation than the tree surface ($\tilde{T}_Y > \tilde{T}_Z$ and/or $\tilde{P}_Y > \tilde{P}_Z$).

Species	Model fit				Optimal climate					
	Seedling (R_Y^2)		Tree (R_Z^2)		Annual mean temperature ($\tilde{T}$, ˚C)			Annual precipitation ($\tilde{P}$, mm)		
	Ecoregion	Plot	Ecoregion	Plot	Seedling	Tree	Hypothesis	Seedling	Tree	Hypothesis
Abies balsamea	0.64	0.15	0.52	0.03	4.56	5.01	Migration	1200	1150	Turnover
Acer pensylvanicum	0.65	0.05	0.58	0.01	5.39	5.95	Migration	1230	1220	Turnover
Acer rubrum	0.11	0.03	0.27	0.08	18.60	7.41	Turnover	1430	1050	Turnover
Acer saccharum	0.50	0.21	0.35	0.06	11.80	11.10	Turnover	1390	1260	Turnover
Betula alleghaniensis	0.68	0.03	0.61	0.02	9.16	6.96	Turnover	1320	1270	Turnover
Betula lenta	0.45	0.03	0.47	0.01	11.40	11.00	Turnover	1450	1340	Turnover
Betula papyrifera	0.36	0.01	0.35	0.01	4.29	4.79	Migration	1020	1080	Migration
Carpinus caroliniana	0.27	0.13	0.14	0.04	18.10	17.50	Turnover	1520	1450	Turnover
Carya alba	0.56	0.02	0.41	0.01	16.10	14.90	Turnover	1380	1320	Turnover
Carya cordiformis	0.49	0.04	0.35	0.01	16.20	11.90	Turnover	1420	1100	Turnover
Carya glabra	0.52	0.01	0.27	0.00	14.70	13.70	Turnover	1280	1270	Turnover
Carya ovata	0.43	0.02	0.38	0.00	17.10	15.10	Turnover	1480	1340	Turnover
Celtis occidentalis	0.36	0.02	0.21	0.00	19.70	18.40	Turnover	1490	1380	Turnover

Cercis canadensis	0.48	0.01	0.44	0.00	18.60	17.30	Turnover	1550	1450	Turnover
Cornus florida	0.60	0.07	0.46	0.00	18.30	17.10	Turnover	1590	1460	Turnover
Diospyros virginiana	0.37	0.01	0.18	0.02	20.10	19.10	Turnover	1610	1500	Turnover
Fagus grandifolia	0.69	0.36	0.43	0.03	11.30	8.53	Turnover	1370	1230	Turnover
Fraxinus americana	0.47	0.05	0.34	0.02	11.80	9.44	Turnover	1210	1120	Turnover
Fraxinus nigra	0.65	0.04	0.54	0.01	5.79	6.40	Migration	777	777	Migration
Fraxinus pennsylvanica	0.43	0.08	0.25	0.00	16.70	11.90	Turnover	1390	811	Turnover
Gleditsia triacanthos	0.14	0.04	0.22	0.05	19.20	18.60	Turnover	1470	1440	Turnover
Ilex opaca	0.38	0.09	0.16	0.02	16.20	17.50	Migration	1340	1480	Migration
Juglans nigra	0.43	0.01	0.49	0.01	14.70	13.20	Turnover	1310	1200	Turnover
Juniperus virginiana	0.42	0.10	0.18	0.01	17.50	16.70	Turnover	1430	1370	Turnover
Liquidambar styraciflua	0.51	0.01	0.48	0.00	18.80	19.10	Migration	1390	1430	Migration
Liriodendron tulipifera	0.46	0.01	0.33	0.03	14.60	13.80	Turnover	1300	1260	Turnover
Maclura pomifera	0.48	0.12	0.30	0.02	16.90	16.40	Turnover	1320	1300	Turnover
Magnolia virginiana	0.39	0.01	0.15	0.04	22.80	21.40	Turnover	1510	1500	Turnover
Morus rubra	0.30	0.07	0.21	0.02	18.20	16.90	Turnover	1550	1510	Turnover
Nyssa sylvatica	0.51	0.02	0.30	0.01	18.50	17.30	Turnover	1610	1480	Turnover
Ostrya virginiana	0.33	0.02	0.17	0.00	16.40	14.40	Turnover	1410	1230	Turnover
Oxydendrum arboreum	0.54	0.01	0.54	0.01	15.30	14.00	Turnover	1410	1330	Turnover
Pinus echinata	0.43	0.05	0.21	0.02	17.40	16.30	Turnover	1480	1400	Turnover
Pinus elliottii	0.39	0.00	0.56	0.00	23.10	22.70	Turnover	1480	1440	Turnover
Pinus palustris	0.49	0.09	0.15	0.00	21.00	20.60	Turnover	1500	1460	Turnover
Pinus resinosa	0.52	0.05	0.29	0.00	6.18	7.35	Migration	799	800	Migration
Pinus strobus	0.45	0.11	0.40	0.01	12.00	11.20	Turnover	1480	1320	Turnover
Pinus taeda	0.77	0.00	0.51	0.00	19.30	18.80	Turnover	1530	1460	Turnover
Pinus virginiana	0.64	0.04	0.44	0.01	15.90	15.40	Turnover	1460	1450	Turnover

Populus deltoides	0.39	0.01	0.20	0.06	19.00	11.10	Turnover	1450	1020	Turnover
Populus grandidentata	0.37	0.01	0.34	0.02	6.70	7.55	Migration	845	858	Migration
Populus tremuloides	0.64	0.03	0.62	0.05	5.17	5.38	Migration	813	822	Migration
Prunus serotina	0.41	0.09	0.32	0.09	11.60	11.10	Turnover	1130	1140	Migration
Quercus alba	0.38	0.06	0.54	0.05	16.80	15.30	Turnover	1570	1410	Turnover
Quercus coccinea	0.55	0.01	0.57	0.02	13.10	13.00	Turnover	1320	1310	Turnover
Quercus falcata	0.48	0.00	0.38	0.01	18.40	17.30	Turnover	1560	1480	Turnover
Quercus laurifolia	0.58	0.12	0.55	0.01	20.60	21.80	Migration	1280	1360	Migration
Quercus macrocarpa	0.32	0.05	0.30	0.02	12.30	11.90	Turnover	1100	1090	Turnover
Quercus marilandica	0.41	0.08	0.15	0.02	19.40	18.20	Turnover	1630	1530	Turnover
Quercus muehlenbergii	0.49	0.02	0.31	0.00	18.20	16.90	Turnover	1490	1430	Turnover
Quercus nigra	0.54	0.02	0.60	0.00	20.60	20.60	Migration	1580	1500	Turnover
Quercus palustris	0.44	0.23	0.17	0.01	8.83	9.03	Migration	861	889	Migration
Quercus phellos	0.45	0.08	0.19	0.01	20.10	19.10	Turnover	1610	1530	Turnover
Quercus prinus	0.62	0.07	0.45	0.00	13.80	13.70	Turnover	1480	1370	Turnover
Quercus rubra	0.28	0.03	0.50	0.04	13.50	12.40	Turnover	1380	1280	Turnover
Quercus stellata	0.49	0.05	0.25	0.07	18.20	17.90	Turnover	1550	1460	Turnover
Quercus velutina	0.46	0.08	0.58	0.05	16.00	15.40	Turnover	1540	1400	Turnover
Robinia pseudoacacia	0.18	0.04	0.42	0.01	10.10	12.30	Migration	1100	1210	Migration
Sassafras albidum	0.40	0.02	0.44	0.04	16.50	15.50	Turnover	1490	1400	Turnover
Thuja occidentalis	0.54	0.12	0.30	0.04	3.85	4.25	Migration	989	893	Turnover
Tilia americana	0.47	0.02	0.52	0.03	10.60	10.60	Migration	1000	937	Turnover
Tsuga canadensis	0.47	0.11	0.55	0.03	12.80	12.50	Turnover	1490	1400	Turnover
Ulmus alata	0.50	0.02	0.30	0.00	20.10	19.20	Turnover	1600	1530	Turnover
Ulmus americana	0.50	0.01	0.31	0.00	17.10	13.90	Turnover	1370	999	Turnover
Ulmus rubra	0.54	0.03	0.30	0.00	19.20	17.10	Turnover	1570	1410	Turnover

Appendix C: Supporting information for Chapter 3

Table C1: Density dependence (DD) effects of per-tree (adult) recruitment (λ) sensitivity to neighboring densities. Mean posterior values follow Figure 3.3.

Species	Conspecific seedling	Heterospecific seedling	Conspecific sapling	Heterospecific sapling	Conspecific tree	Heterospecific tree
Abies balsamea	–0.000001	0.000000	0.000283	–0.000485	–0.001644	–0.000572
Acer pensylvanicum	–0.000003		0.006426	–0.002254		–0.000273
Acer saccharum	–0.000002	–0.000001	–0.000634		–0.000759	–0.000195
Betula alleghaniensis	–0.000002		0.002898		0.001309	–0.00052
Betula lenta	–0.000006			0.002496	0.002683	
Betula papyrifera	–0.000002				–0.002084	–0.000834
Carya alba	–0.000018	–0.000002	0.006695	0.000812		–0.000733
Carpinus caroliniana	–0.000035		0.013315	0.006226	0.031450	
Carya glabra	–0.000023		0.006429	0.003698		
Cercis canadensis	–0.000016	–0.000003	0.004516			–0.001528
Cornus florida	–0.000012	–0.000004	0.004476	0.000879		–0.000586
Diospyros virginiana	–0.000005	–0.000002	0.005612	0.000265		–0.000663
Fagus grandifolia	–0.000002			0.001305		–0.000251
Fraxinus americana	–0.000003	0.000000	0.001731			–0.000364
Fraxinus nigra	–0.000001	–0.000001			–0.000445	–0.000155
Fraxinus pennsylvanica	–0.000011	–0.000002	0.003742		0.001718	0.000424
Ilex opaca	–0.00002	–0.000004		0.002528		
Juniperus virginiana	–0.00001	–0.000003	0.001288		0.000893	–0.000401
Larix laricina	–0.000001	–0.000001	–0.001187		–0.002483	
Liquidambar styraciflua	–0.00001	–0.000003	0.003405			–0.001365

Liriodendron tulipifera	–0.00001	–0.000003				–0.001231
Magnolia virginiana	–0.000051	–0.000005		0.001092		–0.000534
Nyssa sylvatica	–0.000017	–0.000003	0.006068	0.000529		–0.000456
Ostrya virginiana	–0.000005		0.003484			–0.000419
Oxydendrum arboreum	–0.000039		0.012865			–0.000694
Persea borbonia	–0.000012		0.008739		–0.002801	
Picea glauca	–0.000001	0.000000	–0.00208			–0.000659
Picea mariana	–0.000002	0.000000		–0.00038	–0.000733	–0.000553
Picea rubens	–0.000001		0.001203	–0.000574	–0.001787	–0.000736
Pinus strobus	–0.000003	0.000001	0.005382	–0.001228	–0.00111	–0.000487
Pinus taeda		–0.000002	–0.000452		–0.002056	–0.002129
Populus balsamifera	0.000000	0.000000		–0.000687	–0.000494	–0.00042
Populus grandidentata	–0.000001		–0.001513		–0.001141	–0.001252
Populus tremuloides	0.000000	0.000000	–0.000391	–0.000409	–0.001009	–0.000784
Prunus serotina	0.000000	0.000000	0.001610	–0.000575		–0.000594
Quercus alba	–0.000006	–0.000001	0.003964	0.000705	–0.001064	–0.000926
Quercus falcata	–0.000025		0.015711		–0.004533	
Quercus laurifolia	–0.000024			0.003829		–0.000803
Quercus nigra	–0.000017	–0.000001	0.002482	–0.000794		–0.001442
Quercus prinus	–0.000004		0.010549			
Quercus rubra	–0.000004			–0.000495	–0.001133	–0.00066
Quercus stellata	–0.000002		0.005938			–0.00053
Quercus velutina	–0.000002	–0.000001			–0.001232	–0.000776
Sassafras albidum	–0.000011		0.004739			–0.000762
Thuja occidentalis	–0.000001			–0.000298	–0.000094	–0.00042
Tilia americana		–0.000001	0.001389		0.000887	–0.000383

Tsuga canadensis	–0.000009	–0.000001	0.007556	0.003255	–0.002082	0.000557
Ulmus alata	–0.000015	–0.000003			0.004582	–0.000421
Ulmus americana	–0.000009	–0.000001	0.003133			–0.000512
Ulmus rubra	–0.000005		0.008692			0.000117

Table C2: DD effects of per-seedling recruitment (*r*) sensitivity to neighboring densities. Mean posterior values follow Figure 3.4.

Species	Conspecific seedling	Heterospecific seedling	Conspecific sapling	Heterospecific sapling	Conspecific tree	Heterospecific tree
Abies balsamea	0.001495	–0.000438	0.685216	–0.623916	–10.152527	–0.880702
Acer pensylvanicum	0.000373	–0.000089	0.465540	–0.216875	–2.717921	–0.064178
Acer saccharum	0.000291	–0.000228		0.364702	–2.37514	–0.181083
Betula alleghaniensis	0.000696		2.160999		–1.898209	–0.337481
Betula lenta	0.001739			1.102270	–7.265994	–0.53159
Betula papyrifera	0.001273		0.185724		–1.133254	–0.201912
Carya alba	0.007026	–0.000443	2.078961	0.360489	–4.221043	
Carpinus caroliniana	0.002589	–0.002003	1.447005		–12.813295	–0.26734
Carya glabra	0.003797	–0.000976	2.105046	1.123221	–1.703354	
Cercis canadensis	0.001408		0.193516		–0.915273	
Cornus florida	0.000872	–0.000733		0.184379	–4.559856	–0.06502
Diospyros virginiana	0.000653	–0.000022			–0.271844	
Fagus grandifolia	0.000280		0.836752		–2.432262	–0.476224
Fraxinus americana		0.000084	1.258450	0.239139	–2.746002	–0.397204
Fraxinus nigra	0.001074	–0.000379		0.247805	–3.129372	–0.14963
Fraxinus pennsylvanica	0.000607		2.805987		–6.51034	0.193874
Ilex opaca		–0.001313		0.651033	–11.400692	
Juniperus virginiana	0.002330	–0.001842	0.651939	0.401926	–2.612161	
Larix laricina	0.000456		–0.082946	–0.182532	–1.155773	–0.210636
Liquidambar styraciflua	0.004299	–0.001174	1.876632		–5.912261	–0.506512
Liriodendron tulipifera	0.004435	–0.000493	1.330953	0.225246	–2.399157	–0.174708
Magnolia virginiana			–2.396341	3.670378	–5.529313	–0.794229
Nyssa sylvatica	0.003131	–0.001115	1.787039		–5.149239	–0.145544

Ostrya virginiana	0.000631			–0.259582	–5.344183	
Oxydendrum arboreum	0.008293	–0.000569	1.769477	0.845719	–6.894476	
Persea borbonia			4.180085	1.172282	–9.178238	–0.126049
Picea glauca	0.000822	–0.000094			–1.109422	–0.182388
Picea mariana	0.000072	–0.000098		–0.070777	–0.850646	–0.341989
Picea rubens	0.000719			–0.809953	–2.494183	–1.093352
Pinus strobus	0.001267	0.000199	1.543376	–0.479631	–2.458429	–0.326716
Pinus taeda	0.000574	–0.000139	0.178925		–0.708064	–0.463407
Populus balsamifera		0.000080		–0.17809	–0.419009	–0.173052
Populus grandidentata	0.000820		0.080488	–0.171183	–0.432901	–0.100751
Populus tremuloides	0.000904	–0.000042	–0.227766	–0.374673	–1.74764	–0.523146
Prunus serotina	0.001049	–0.000264	1.702818		–2.967515	–0.379167
Quercus alba	0.000744		1.569810	0.487794	–1.193106	–0.175399
Quercus falcata	0.007006		2.483738	0.365345	–3.39118	
Quercus laurifolia	0.002490		0.922236	0.726606	–0.85833	–0.158407
Quercus nigra	0.004014	–0.000933	0.598746		–3.986119	–0.435269
Quercus prinus	0.001412	–0.000162	1.172363	0.352854	–0.357124	–0.159861
Quercus rubra	0.000629		0.505340		–0.800017	–0.149551
Quercus stellata	0.001122	–0.000311	0.845371		–0.536761	–0.128366
Quercus velutina	0.001383		1.531913		–1.436324	–0.16344
Sassafras albidum		0.000390		–1.2909	–5.434257	–0.346966
Thuja occidentalis	0.000098	–0.000029	0.054807		–0.271949	–0.238601
Tilia americana	0.002953	–0.000339	1.987157		–3.676451	–0.414057
Tsuga canadensis	0.001605		2.438694	0.450666	–1.646037	0.172604
Ulmus alata	0.004432	–0.001056	1.240229		–4.686711	–0.113974
Ulmus americana	0.000755	–0.000283	1.452662		–2.6686	0.059276

Ulmus rubra	4.352615	0.445098	–3.207558

References

Agee JK (1993) *Fire Ecology of Pacific Northwest Forests,* Washington, DC, Island Press.

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters,* **14**, 677-689.

Antonovics J, Levin DA (1980) The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics,* **11**, 411-452.

Assmann E (1970) *The Principles of Forest Yield Study,* New York, NY, Pergamon Press.

Bagchi R, Gallery RE, Gripenberg S *et al.* (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature,* **506**, 85-88.

Bagchi R, Swinfield T, Gallery RE, Lewis OT, Gripenberg S, Narayan L, Freckleton RP (2010) Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters,* **13**, 1262-1269.

Bai XJ, Queenborough SA, Wang XG *et al.* (2012) Effects of local biotic neighbors and habitat heterogeneity on tree and shrub seedling survival in an old-growth temperate forest. *Oecologia,* **170**, 755-765.

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology,* **8**, 390-407.

Banerjee S, Carlin BP, Gelfand AE (2004) *Hierarchical Modeling and Analysis for Spatial Data,* Boca Raton, FL, Chapman & Hall/CRC.

Bansal S, Germino MJ (2010) Variation in ecophysiological properties among conifers at an ecotonal boundary: comparison of establishing seedlings and established adults at timberline. *Journal of Vegetation Science,* **21**, 133-142.

Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions,* **15**, 409-420.

Bechtold WA, Patterson PL (2005) *The Enhanced Forest Inventory and Analysis Program: National Sampling Design and Estimation Procedures,* Asheville, NC, USDA Forest Service, Southern Research Station.

Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences,* **105**, 4197-4202.

Bell DM, Bradford JB, Lauenroth WK (2014) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography,* **23**, 168-180.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters,* **15**, 365-377.

Bergamini A, Ungricht S, Hofmann H (2009) An elevational shift of cryophilous bryophytes in the last century - an effect of climate warming? *Diversity and Distributions,* **15**, 871-879.

Bertrand R, Gégout J-C, Bontemps J-D (2011) Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. *Oikos,* **120**, 1479-1488.

Botkin DB, Saxe H, Araujo MB *et al.* (2007) Forecasting the effects of global warming on biodiversity. *BioScience,* **57**, 227-236.

Boucher-Lalonde V, Morin A, Currie DJ (2012) How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography,* **21**, 1157-1166.

Broennimann O, Thuiller W, Hughes G, Midgley GF, Alkemade JMR, Guisan A (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology,* **12**, 1079-1093.

Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters,* **10**, 701-709.

Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics,* **27**, 597-623.

Butterfield BJ, Briggs JM (2011) Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia,* **165**, 477-487.

Bykova O, Chuine I, Morin X, Higgins SI (2012) Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography,* **39**, 2191-2200.

Canham CD, Thomas RQ (2010) Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. *Ecology,* **91**, 3433-3440.

Cavender-Bares J, Bazzaz FA (2000) Changes in drought response strategies with ontogeny in Quercus rubra: implications for scaling from seedlings to mature trees. *Oecologia,* **124**, 8-18.

Chase JM, Leibold MA (2003) *Ecological Niches: Linking Classical and Contemporary Approaches,* Chicago, IL, University of Chicago Press.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science,* **333**, 1024-1026.

Chen L, Mi XC, Comita LS, Zhang LW, Ren HB, Ma KP (2010) Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest. *Ecology Letters,* **13**, 695-704.

Chesson P (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics,* **31**, 343-366.

Clark JS (1990) Integration of ecological levels: individual plant growth, population mortality and ecosystem processes. *Journal of Ecology,* **78**, 275-299.

Clark JS (1991) Disturbance and tree life history on the shifting mosaic landscape. *Ecology,* **72**, 1102-1118.

Clark JS (1996) Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *American Naturalist,* **148**, 976-996.

Clark JS (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist,* **152**, 204-224.

Clark JS (2010) Individuals and the variation needed for high species diversity in forest trees. *Science,* **327**, 1129-1132.

Clark JS, Bell DM, Hersh MH *et al.* (2011a) Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecology Letters,* **14**, 1273-1287.

Clark JS, Bell DM, Hersh MH, Nichols L (2011b) Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. *Global Change Biology,* **17**, 1834-1849.

Clark JS, Bell DM, Kwit M, Stine A, Vierra B, Zhu K (2012) Individual-scale inference to anticipate climate-change vulnerability of biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **367**, 236-246.

Clark JS, Lewis M, Horvath L (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist,* **157**, 537-554.

Clark JS, Lewis M, McLachlan JS, HilleRisLambers J (2003) Estimating population spread: what can we forecast and how well? *Ecology,* **84**, 1979-1988.

Cleland DT, Avers PE, McNab WH, Jensen ME, Bailey RG, King T, Russell WE (1997) National hierarchical framework of ecological units. In: *Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources.* (eds Boyce MS, Haney A) pp 181-200. New Haven, CT, Yale University Press.

Comita LS, Hubbell SP (2009) Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology,* **90**, 328-334.

Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP (2010) Asymmetric density dependence shapes species abundances in a tropical tree community. *Science,* **329**, 330-332.

Condit R, Hubbell SP, Foster RB (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist,* **140**, 261-286.

Condit R, Hubbell SP, Foster RB (1994) Density dependence in two understory tree species in a neotropical forest. *Ecology,* **75**, 671-680.

Connell JH (1970) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Population.* (eds Den Boer PJ, Gradwell GR) pp 298-310. Wageningen, Proceedings of the Advanced Study Institute, Centre for Agricultural Publishing and Documentation.

Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? *Trends in Ecology and Evolution,* **28**, 482-488.

Cox CB, Moore PD (2010) *Biogeography: An Ecological and Evolutionary Approach,* Hoboken, NJ, Wiley.

Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science,* **331**, 324-327.

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to Quaternary climate change. *Science,* **292**, 673-679.

Diez JM, Pulliam HR (2007) Hierarchical analysis of species distributions and abundance across environmental gradients. *Ecology,* **88**, 3144-3152.

Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology,* **17**, 1022-1035.

Dobzhansky T (1950) Evolution in the tropics. *American Scientist,* **38**, 209-221.

Donovan LA, Ehleringer JR (1991) Ecophysiological differences among juvenile and reproductive plants of several woody species. *Oecologia,* **86**, 594-597.

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics,* **40**, 677-697.

Eriksson O (2002) Ontogenetic niche shifts and their implications for recruitment in three clonal Vaccinium shrubs: Vaccinium myrtillus, Vaccinium vitis-idaea, and Vaccinium oxycoccos. *Canadian Journal of Botany,* **80**, 635-641.

Fastie CL (1995) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology,* **76**, 1899-1916.

Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L (2013) Modeling plant species distributions under future climates: how fine-scale do climate projections need to be? *Global Change Biology,* **19**, 473-483.

Gallagher RV, Beaumont LJ, Hughes L, Leishman MR (2010) Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *Journal of Ecology,* **98**, 790-799.

Gottfried M, Pauli H, Futschik A *et al.* (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change,* **2**, 111-115.

Gripenberg S, Bagchi R, Gallery RE, Freckleton RP, Narayan L, Lewis OT (2014) Testing for enemy-mediated density-dependence in the mortality of seedlings: field experiments with five Neotropical tree species. *Oikos,* **123**, 185-193.

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews,* **52**, 107-145.

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters,* **8**, 993-1009.

Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature,* **430**, 71-75.

Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature,* **404**, 493-495.

Harper JL (1977) *Population Biology of Plants,* London, UK, Academic Press.

Harper JL, White J (1974) The demography of plants. *Annual Review of Ecology and Systematics,* **5**, 419-463.

He FL, Duncan RP (2000) Density-dependent effects on tree survival in an old-growth Douglas fir forest. *Journal of Ecology,* **88**, 676-688.

Heikkinen RK, Luoto M, Araujo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography,* **30**, 751-777.

Herault B, Bachelot B, Poorter L *et al.* (2011) Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology,* **99**, 1431-1440.

Herrando-Perez S, Delean S, Brook BW, Bradshaw CJA (2012) Density dependence: an ecological Tower of Babel. *Oecologia,* **170**, 585-603.

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics,* **43**, 227-248.

HilleRisLambers J, Clark JS, Beckage B (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature,* **417**, 732-735.

Hof C, Levinsky I, Araujo MB, Rahbek C (2011) Rethinking species' ability to cope with rapid climate change. *Global Change Biology,* **17**, 2987-2990.

Holzinger B, Hulber K, Camenisch M, Grabherr G (2008) Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology,* **195**, 179-196.

Houter NC, Pons TL (2012) Ontogenetic changes in leaf traits of tropical rainforest trees differing in juvenile light requirement. *Oecologia,* **169**, 33-45.

Hubbell SP, Ahumada JA, Condit R, Foster RB (2001) Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research,* **16**, 859-875.

Hubbell SP, Condit R, Foster RB (1990) Presence and absence of density dependence in a neotropical tree community. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **330**, 269-281.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution,* **15**, 56-61.

Ibanez I, Clark JS, Dietze MC (2008) Evaluating the sources of potential migrant species: implications under climate change. *Ecological Applications,* **18**, 1664-1678.

Ibanez I, Clark JS, Dietze MC (2009) Estimating colonization potential of migrant tree species. *Global Change Biology,* **15**, 1173-1188.

IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change,* Cambridge, UK and New York, NY, USA, Cambridge University Press.

Iverson LR, Prasad AM (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs,* **68**, 465-485.

Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management,* **254**, 390-406.

Iverson LR, Schwartz MW, Prasad AM (2004) How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography,* **13**, 209-219.

Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences,* **106**, 19685-19692.

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist,* **104**, 501-528.

Johnson DJ, Beaulieu WT, Bever JD, Clay K (2012) Conspecific negative density dependence and forest diversity. *Science,* **336**, 904-907.

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences,* **105**, 11823-11826.

Keys JE, Cleland DT, McNab WH (2007) *Delineation, Peer Review, and Refinement of Subregions of the Conterminous United States,* Washington, DC, USDA Forest Service.

Kobe RK, Vriesendorp CF (2011) Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters,* **14**, 503-510.

Kulmatiski A, Beard KH (2013) Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia,* **171**, 25-37.

Lambert D (1992) Zero-inflated Poisson regression, with an application to defects in manufacturing. *Technometrics,* **34**, 1-14.

le Roux PC, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. *Global Change Biology,* **14**, 2950-2962.

Lebrija-Trejos E, Wright SJ, Hernández A, Reich PB (2013) Does relatedness matter? Phylogenetic density dependent survival of seedlings in a tropical forest. *Ecology*.

Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science,* **320**, 1768-1771.

Lenoir J, Gegout JC, Pierrat JC, Bontemps JD, Dhote JF (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). *Ecography,* **32**, 765-777.

Lewis MA, Neubert MG, Caswell H, Clark JS, Shea K (2006) A guide to calculating discrete-time invasion rates from data. In: *Conceptual Ecology and Invasions Biology: Reciprocal Approaches To Nature.* (eds Cadotte MW, McMahon SM, Fukami T) pp 169-192. Dordrecht, Netherlands, Springer.

Lewis SL, Malhi Y, Phillips OL (2004a) Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **359**, 437-462.

Lewis SL, Phillips OL, Baker TR *et al.* (2004b) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **359**, 421-436.

Lin LX, Comita LS, Zheng Z, Cao M (2012) Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *Journal of Ecology,* **100**, 905-914.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature,* **462**, 1052-1055.

MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist,* **101**, 377-385.

MacArthur RH (1972) *Geographical Ecology,* New York, NY, Harper & Row, Publishers.

Maiorano L, Cheddadi R, Zimmermann NE *et al.* (2013) Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. *Global Ecology and Biogeography,* **22**, 302–317.

McCarty JP (2001) Ecological consequences of recent climate change. *Conservation Biology,* **15**, 320-331.

McGill BJ (2010) Matters of scale. *Science,* **328**, 575-576.

McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF (2007) Potential impacts of climate change on the distribution of North American trees. *BioScience,* **57**, 939-948.

McLaughlin BC, Zavaleta ES (2012) Predicting species responses to climate change: demography and climate microrefugia in California valley oak (Quercus lobata). *Global Change Biology,* **18**, 2301-2312.

McMahon SM, Harrison SP, Armbruster WS *et al.* (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology and Evolution,* **26**, 249-259.

McNab WH, Cleland DT, Freeouf JA, J. E. Keys J, Nowacki GJ, Carpenter CA (2007) *Description of "Ecological Subregions: Sections of the Conterminous United States",* Washington, DC, USDA Forest Service.

McRoberts RE, Holden GR, Nelson MD *et al.* (2005) Estimating and circumventing the effects of perturbing and swapping inventory plot locations. *Journal of Forestry,* **103**, 275-279.

Meier ES, Lischke H, Schmatz DR, Zimmermann NE (2011) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, DOI: 10.1111/j.1466-8238.2011.00669.x.

Metz MR, Sousa WP, Valencia R (2010) Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology,* **91**, 3675-3685.

Midgley GF, Hannah L, Millar D, Rutherford MC, Powrie LW (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography,* **11**, 445-451.

Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology,* **94**, 973-979.

Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology,* **25**, 693-712.

Mok H-F, Arndt SK, Nitschke CR (2012) Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of South-Eastern Australia. *Global Change Biology,* **18**, 1053-1072.

Murphy HT, VanDerWal J, Lovett-Doust J (2006) Distribution of abundance across the range in eastern North American trees. *Global Ecology and Biogeography,* **15**, 63-71.

Murphy HT, VanDerWal J, Lovett-Doust J (2010) Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters,* **13**, 1233-1244.

Nathan R, Horvitz N, He Y, Kuparinen A, Schurr FM, Katul GG (2011) Spread of North American wind-dispersed trees in future environments. *Ecology Letters,* **14**, 211-219.

Neubert MG, Caswell H (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology,* **81**, 1613-1628.

Newbery DM, Stoll P (2013) Relaxation of species-specific neighborhood effects in Bornean rain forest under climatic perturbation. *Ecology,* **94**, 2838-2851.

Paine CET, Norden N, Chave J, Forget PM, Fortunel C, Dexter KG, Baraloto C (2012) Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters,* **15**, 34-41.

Palow DT, Nolting K, Kitajima K (2012) Functional trait divergence of juveniles and adults of nine Inga species with contrasting soil preference in a tropical rain forest. *Functional Ecology,* **26**, 1144–1152.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics,* **37**, 637-669.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421**, 37-42.

Parrish JAD, Bazzaz FA (1985) Ontogenetic niche shifts in old-field annuals. *Ecology,* **66**, 1296-1302.

Pauli H, Gottfried M, Dullinger S *et al.* (2012) Recent plant diversity changes on Europe's mountain summits. *Science,* **336**, 353-355.

Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. *Trends in Ecology and Evolution,* **23**, 149-158.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography,* **12**, 361-371.

Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography,* **27**, 285-298.

Peters HA (2003) Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters,* **6**, 757-765.

Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography,* **38**, 817-827.

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) *Ecological Niches and Geographic Distributions,* Princeton, NJ, Princeton University Press.

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. *Science,* **335**, 1344-1348.

Phillips OL, Baker TR, Arroyo L *et al.* (2004) Pattern and process in Amazon tree turnover, 1976-2001. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **359**, 381-407.

Phillips OL, Gentry AH (1994) Increasing turnover through time in tropical forests. *Science,* **263**, 954-958.

Piao T, Comita LS, Jin GZ, Kim JH (2013) Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia,* **172**, 207-217.

Pollard JE, Westfall JA, Patterson PL, Gartner DL, Hansen M, Kuegler O (2006) *Forest Inventory and Analysis National Data Quality Assessment Report for 2000 to 2003,* Fort Collins, CO, USDA Forest Service, Rocky Mountain Research Station.

Poorter L (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology,* **13**, 396-410.

Pulliam HR (1988) Sources, sinks, and population regulation. *American Naturalist,* **132**, 652-661.

Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters,* **3**, 349-361.

Queenborough SA, Burslem DFRP, Garwood NC, Valencia R (2007) Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology,* **88**, 2248-2258.

Quero JL, Gomez-Aparicio L, Zamora R, Maestre FT (2008) Shifts in the regeneration niche of an endangered tree (Acer opalus ssp granatense) during ontogeny: using an ecological concept for application. *Basic and Applied Ecology,* **9**, 635-644.

R Development Core Team (2010 – 2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Randin CF, Engler R, Normand S *et al.* (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology,* **15**, 1557-1569.

Saxe H, Cannell MGR, Johnsen B, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist,* **149**, 369-399.

Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (eds) (2002) *Predicting Species Occurrences: Issues of Accuracy and Scale,* Washington, DC, Island Press.

Seo C, Thorne JH, Hannah L, Thuiller W (2009) Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters,* **5**, 39-43.

Sheffer E, Canham CD, Kigel J, Perevolotsky A (2013) Landscape-scale density-dependent recruitment of oaks in planted forests: more is not always better. *Ecology,* **94**, 1718-1728.

Smith WB, Miles PD, Perry CH, Pugh SA (2009) *Forest Resources of the United States, 2007,* Washington, DC, USDA Forest Service, Washington Office.

Soberon J, Nakamura M (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences,* **106**, 19644-19650.

Stephenson NL, van Mantgem PJ (2005) Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters,* **8**, 524-531.

Stohlgren TJ, Bachand RR, Onami Y, Binkley D (1998) Species-environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. *Plant Ecology,* **135**, 215-228.

Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *The American Naturalist,* **179**, 303-314.

Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature,* **427**, 145-148.

Thomas SC, Winner WE (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology,* **22**, 117-127.

Thuiller W, Lavorel S, Araujo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences,* **102**, 8245-8250.

Trivedi MR, Berry PM, Morecroft MD, Dawson TP (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology,* **14**, 1089-1103.

Urbieta IR, Garcia LV, Zavala MA, Maranon T (2011) Mediterranean pine and oak distribution in southern Spain: is there a mismatch between regeneration and adult distribution? *Journal of Vegetation Science,* **22**, 18-31.

Uriarte M, Condit R, Canham CD, Hubbell SP (2004) A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology,* **92**, 348-360.

USDA Forest Service (2011) *Forest Inventory and Analysis Fiscal Year 2010 Business Report,* Washington, DC, U.S. Department of Agriculture.

USDA NRCS (2010) The PLANTS Database, National Plant Data Center, Baton Rouge, LA 70874-4490 USA. http://plants.usda.gov

USGS (1999) Digital Representations of Tree Species Range Maps from "Atlas of United States Trees" by Elbert L. Little, Jr. http://esp.cr.usgs.gov/data/atlas/little/

Van Bogaert R, Haneca K, Hoogesteger J, Jonasson C, De Dapper M, Callaghan TV (2011) A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography,* **38**, 907-921.

Walther GR, Berger S, Sykes MT (2005) An ecological 'footprint' of climate change. *Proceedings of the Royal Society B: Biological Sciences,* **272**, 1427-1432.

Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature,* **416**, 389-395.

Warren RJ, Bradford MA (2011) The shape of things to come: woodland herb niche contraction begins during recruitment in mesic forest microhabitat. *Proceedings of the Royal Society B: Biological Sciences,* **278**, 1390-1398.

Webb CO, Peart DR (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology,* **80**, 2006-2017.

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics,* **15**, 393-425.

Wiens JJ (2011) The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **366**, 2336-2350.

Wiens JJ, Ackerly DD, Allen AP *et al.* (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters,* **13**, 1310-1324.

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics,* **36**, 519-539.

Wills C, Condit R (1999) Similar non-random processes maintain diversity in two tropical rainforests. *Proceedings of the Royal Society B: Biological Sciences,* **266**, 1445-1452.

Wills C, Condit R, Foster RB, Hubbell SP (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences,* **94**, 1252-1257.

Woodall CW, Oswalt CM, Westfall JA, Perry CH, Nelson MD, Finley AO (2009) An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management,* **257**, 1434-1444.

Woodall CW, Oswalt CM, Westfall JA, Perry CH, Nelson MD, Finley AO (2010) Selecting tree species for testing climate change migration hypotheses using forest inventory data. *Forest Ecology and Management,* **259**, 778-785.

Woodall CW, Zhu K, Westfall JA, Oswalt CM, D'Amato AW, Walters BF, Lintz HE (2013) Assessing the stability of tree ranges and influence of disturbance in eastern US forests. *Forest Ecology and Management,* **291**, 172-180.

Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters,* **13**, 1-10.

Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters,* **8**, 662-673.

Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology,* **18**, 1042-1052.

Zhu K, Woodall CW, Ghosh S, Gelfand AE, Clark JS (2014) Dual impacts of climate change: forest migration and turnover through life history. *Global Change Biology,* **20**, 251-264.

Biography

Kai Zhu was born in Nanchang, Jiangxi, China on August 30, 1984. He received a B.S. degree in Management Sciences (Systems Theory) in 2006 and a M.S. degree in Natural Resources (Ecology) in 2009 from Beijing Normal University, China. In 2009, he began Ph.D. program in Environment (Ecology) and M.S. program in Statistical Science at Duke University.

While at Duke University, Kai Zhu published a number of journal articles and book chapters. First-authored publications include "Failure to migrate: lack of tree range expansion in response to climate change" and "Dual impacts of climate change: forest migration and turnover through life history," both in *Global Change Biology*; "New approaches to FIA data for understanding distribution, abundance, and response to climate change" in *Moving from Status to Trends: Forest Inventory and Analysis (FIA) Symposium 2012*. Co-authored publications include "Individual-scale variation, species-scale differences: inference needed to understand diversity" (*Ecology Letters*); "Individual-scale inference to anticipate climate-change vulnerability of biodiversity" (*Philosophical Transactions of the Royal Society B: Biological Sciences*); "The k-ZIG: flexible modeling for zero-inflated counts" (*Biometrics*); "Dynamic inverse prediction and sensitivity analysis with high-dimensional responses: application to climate-change vulnerability of biodiversity" (*Journal of Agricultural, Biological, and Environmental Statistics*); "Competition-interaction landscapes for the joint response of forests to climate change" (*Global Change Biology*); "More than the sum of the parts: forest climate response from joint species distribution models" (*Ecological Applications*).

In 2013, Kai Zhu received a Doctoral Dissertation Improvement Grant (DDIG) from the National Science Foundation (NSF). In 2012, he was the recipient of Annual Outstanding Student

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